ASPECTS OF THE BEHAVIOUR OF THE SOUTH ISLAND FANTAIL *Rhipidura fuliginosa fuliginosa*

A thesis

presented for the degree of

Master of Science

in the

University of Canterbury,

Christchurch, New Zealand.

by

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September 1977.

The South Island Fantail

Rhipidura fuliginosa fuliginosa

When despair for the world grows in me and I wake in the night at the least sound in fear of what my wife and my children's lives may be, I go and lie down where the wood drake rests in his beauty on the water, and the great heron feeds. I come into the peace of wild things who do not tax their lives with forethought of grief. I come into the presence of still water. And I feel above me the day-blind stars waiting with their light. For a time I rest in the grace of the world and am free.

Wendell Berry.

To

Nikki.

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CHAPTER 1

CHAPTER 1

INTRODUCTION

The fantail is a small passerine belonging to the family Muscicapidae (subfamily Muscicapinae), which also contains such birds as tits, robins and flycatchers. The fantails of the genus *Rhipidura* inhabit Australia, New Guinea, the Philippines, parts of South-East Asia, New Zealand and many remote islands of the Pacific (Gilliard 1958). The New Zealand Fantail is divided into three subspecies which are dimorphic, with pied and black phases which freely interbreed. This study is concerned with the subspecies *Rhipidura fuliginosa fulginosa* (the South Island Fantail).

Although the New Zealand Fantail is common throughout its range, very little information is available on its biology and behaviour. The few studies undertaken in New Zealand have been concerned with plumage patterns, particularly with respect to differences between pied and black phases (Fleming 1949, Soper 1964, Kinsky 1965). In a related study, Caughley (1969) studed the genetics of melanism in the fantail. The only study which provided some insight into the behaviour of this bird was undertaken by Blackburn (1965); his work was on the North Island Fantail and was mainly concerned with the breeding biology of the subspecies rather than the behaviour. A few notes on the sighting of fantails, or brief descriptions on the nesting and re-use of nests by New Zealand Fantails have been published (Moncrieff 1931, Fleming 1949, Cunningham 1954, Blackburn 1966, Coates 1966, Flux 1974).

A similar lack of information on Australian Fantails exists. A detailed study on the analysis of nest-records of the Willie Wagtail

Rhipidura leucophyrs has been undertaken (Marchant 1974). However, it did not provide much information on the behaviour of this species. A few records of the sighting of fantails (Chaffer 1939, Wakefield 1963, Heatwole 1968) and nest-building (Roberts 1942, Roberts 1945, Brown 1949) have been made. A description of a courtship display in the Willie Wagtail (Hough 1969) and two papers on the evolution of fantail flycatchers (Mayr and Moynihan 1946, Harrison 1976) were found in my literature research.

This thesis aims to fill the gaps in the knowledge already available on aspects of the behaviour of the South Island Fantail. A detailed description of the breeding behaviour, including the displays (Chapter four), nest-building behaviour (Chapter five), incubation behaviour (Chapter six) and parental behaviour (Chapter seven), follows an outline of the behaviour patterns throughout a 12 month period (Chapter three). A discussion of various non-breeding activities, that is, feeding and other maintenance activities, vocalisation patterns and inter-specific interaction is given in Chapters eight, nine, ten and eleven, respectively.

However, the main objective of this study is to elucidate the nature and function of tail flicking and fanning by the fantail (Chapter twelve). Although fanning and flicking have been mentioned by several ornithologists (Anderson 1926, Westerkov 1967) their descriptions appear to be very vague and provide little information as to the function of fanning and flicking. A review of the literature on tail fanning and flicking in small passerines provides some indication as to the possible functions. These include:-

1) a distraction display, which parent birds perform in response to a predator. The display simulates an incapacity as a result of injury, and functions in diverting the attention of the predator

from the nest or the young. The principle movements of the display consist of fanning, beating or dragging one or both wings, spreading or depressing the tail, fluffing of the feathers and the production of distress calls (Pettingill 1970),

2) a mobbing response. In any season, groups of small birds respond to a perching hawk or owl by mobbing it. The mobbing response in the chaffinch was investigated in detail by Hinde (1954). During the response, the chaffinch perches facing the predator and calls in a characteristic manner. The body posture involved in the mobbing response consists of the following components:-

   a) crest raised,

   b) legs slightly flexed,

   c) wings raised from supporting feathers,

   d) body movement from side-to-side,

   e) movement of the tail up and down.

   Hinde noted that the response may serve to put all birds in a given area on the alert, and to recruit other chaffinches into the area,

3) courtship display. During the courtship displays of the male Red-vented Hermit *Phaethornis ruber* (a humming bird) the tail is fanned and flicked in a characteristic manner (Davis 1958).

4) aggressive displays. Pied Flycatchers *Muscicapa hypoleuca* territory owners threaten intruding conspecifics by fluffing their feathers and flicking their tails (Von Haartman 1956), or

5) a method used to facilitate prey capture. Warham (1956) suggested that the flicking of the tail in the Willie Wagtail may function to frighten insect prey into flight. Insect flushing is also thought to be the function of tail fanning and flicking in the Australian Grey Fantail *Rhipidura fuliginosa* (Harrison 1976).

By studying distraction displays, mobbing responses, courtship and aggressive displays and feeding behaviour in the South Island Fantail the function of tail fanning and flicking in this species may become evident.

In any behavioural study a researcher must know thoroughly the behavioural make-up of his subject before designating functions to particular behavioural components. Consequently the study of "Tail fanning" and "Tail flicking" in the fantail would have been impossible without a study on the general behaviour of the South Island Fantail.

CHAPTER 2

CHAPTER 2

METHODS AND STUDY AREAS

2.1 INTRODUCTION

The study of the "Aspects of the Behaviour of the South Island Fantail" was undertaken between March 1975 and March 1976. For ten months, approximately six hours per day, six days per week, were spent in the field. In June and July (i.e., mid-winter) less time was spent in the field and more time in the laboratory analysing cinematographic films.

The results of this study are based on approximately 1,440 hours of fieldwork.

2.2 POPULATION SIZE

Observations from March to June (1975) were made of approximately 20 birds, but during the winter months (June to August) the number decreased to an estimated eight birds. By August only two pairs were located in Riccarton Bush but another two were found in Hagley Park. From January to March (1976) a population totalling approximately 30 birds (from both localities) was observed. A brief study of five pairs at Kowhai Bush, Kaikoura, supplemented the investigation of breeding behaviour.

A study of some aspects of the breeding behaviour of the fantail could only be made on four pairs of birds. Although more breeding birds could have been found in other areas around Christchurch, I found six hours a day insufficient to study only four pairs. I decided that

better results would be obtained by sitting for long periods at a few nests rather than short periods at many nests. Many studies of the breeding biology and behaviour of other passerine species have been based on two or three breeding pairs (Schantz 1939, Pitelka 1940, Betts 1955, Gibb 1955, Anderson and Anderson 1962, Hartshorne 1962, Royama 1966).

2.3 GENERAL STUDY PROCEDURES

The science of behaviour (ethology) is essentially the study of animal activities by direct observation, supplemented by experimental methods (Pettingill 1970). This study was concerned solely with direct observations. With the limited time available in which to complete this study, and the difficulties involved in keeping small passerines in captivity, experimental work was not feasible.

Direct observations were recorded on a portable tape-recorder during the first five months of the study, but because of the very long periods involved in analysing the tapes it became impractical to continue with this mode of recording observations once the breeding season began, when more time was spent observing rather than finding and following birds. Consequently, most of the breeding behaviour was noted in a field-book - I continued to use the tape-recorder to describe displays and record vocalisations. In most cases the following points were noted during all observations:-

(i) the sex of the bird,

(ii) the behaviour of the fantail,

(iii) body postures, position of the wings and tail, amount of tail and/or wing fanning,

(iv) type of vocalisation,

(v) height of bird above the ground,

(vi) presence or absence of other fantails, and

(vii) the behaviour or response of other fantails when present.

By continuously recording this information when the fantails were present I obtained information on the general sequences of behaviour which could be analysed later for:-

(i) descriptions of particular components of the sequence,

(ii) information on events which immediately precede specific components, acts or other behavioural events, and

(iii) the effect of various behavioural acts on the general behaviour of the bird performing the acts and others nearby.

Stop-watches were used to record such aspects as the time spent building, and time spent on and off the nest during the incubation period. Prepared data sheets and use of symbols provided a very quick method of recording the number of behavioural sequences and other aspects of the behaviour of the South Island Fantail.

A hide was not used in this study. In the breeding season I sat quietly within 4.5 metres of the nest and noted the behaviour of the fantails at and around the nest. The birds did not appear to be disturbed by my presence and rarely approached or gave alarm calls close-by. In the non-breeding season (January to August) I followed the fantails through the bush to observe the feeding methods and mode of locomotion as the fantails foraged. These observations were vital to the study of tail fanning and flicking and could not have been made if my movements had been restricted by the use of a hide.

With such a small population size I did not want to risk disturbing and possibly losing the breeding pairs by mist-netting. The birds were identified by individual differences in plumage, either in coloration or the presence of broken rectrices. As soon as the fantails started incubating their first clutch, the undersides of the

adults' rectrices were marked with a red quick-drying enamel paint by using a paint brush attached to a long pole. These markings lasted during the breeding season until the adults moulted.

The identification of the sexes was based on behavioural criteria, particularly on differences in vocalisation. In each pair it became obvious that only one of the pair sang to any great extent (Section 11.3.3). By noting the behaviour of the bird singing I assumed this bird to be the male. Many studies on other passerines have found that the bird that sang a large amount was usually the male (Van Tyne and Berger 1959, Thorpe 1961, Thomson 1964).

Great difficulty was encountered in obtaining photographs and cinematographic information of the fantails' movements because the activities of this species were so quick. Although a number of cine-films were taken by me and by Terry Williams (Canterbury University, Zoology Department photographer), most of the sketches which supplement this thesis were obtained from a frame-by-frame analysis of a production by the New Zealand National Film Unit, called "The Legend of the Birds". I hope to obtain photographs of the displays described in Chapter four in the very near future.

Detailed descriptions of the methods specifically related to each aspect of behaviour studied are given at the beginning of most chapters.

A number of points must be borne in mind when reading this thesis. These are:-

(i) times of the day are given in New Zealand Standard Time,

(ii) such notations as the 25/10/75 refer to the 25th day of the tenth month of 1975,

(iii) abbreviations for each pair studied are used throughout the thesis. P1R refers to Pair 1 Riccarton Bush, P2R refers to

Pair 2 Riccarton Bush, P1B symbolises Pair 1 Botanical Gardens and P2B to Pair 2 Botanical Gardens,

(iv) a statistical treatment of my quantitative data has been made on only those results which I feel are particularly important. Results from which Chi-square values have been calculated can be found in the appropriate tables. Raw data from which t-test values were obtained are given in the Appendix. In many cases I have calculated t-tests on the results of only one pair. However, this was only done if the results of the other pairs were similar and, consequently, would have had similar t-test values.

2.4 MAIN STUDY AREAS

2.4.1 Riccarton Bush

The main area of Riccarton Bush is approximately 6.2 hectares. The bush is the sole surviving remnant of those swamp forests which once flourished near the city of Christchurch and northwards along the coast of Canterbury. The land in Riccarton Bush has been occupied by swamp forest for many hundreds of years.

According to their heights the plants of Riccarton Bush may be said to belong to one of four different tiers, namely:- the tall trees, forming the canopy of the forest; the smaller trees; the shrubs; and finally, the forest floor.

Most of the tall forest trees are Taxadas, members of the Yew family, and are known as the White Pine *(Podocarpus dacrydioides)*, Black Pine *(P. spicatus)*, and the totara *(P. totara)*. The White Pine, Kahikatea, is the most numerous and hence the alternative name often given to this class of forest: Kahikatea forest. The White Pines grow closely together and attain a great size, their trunks often being

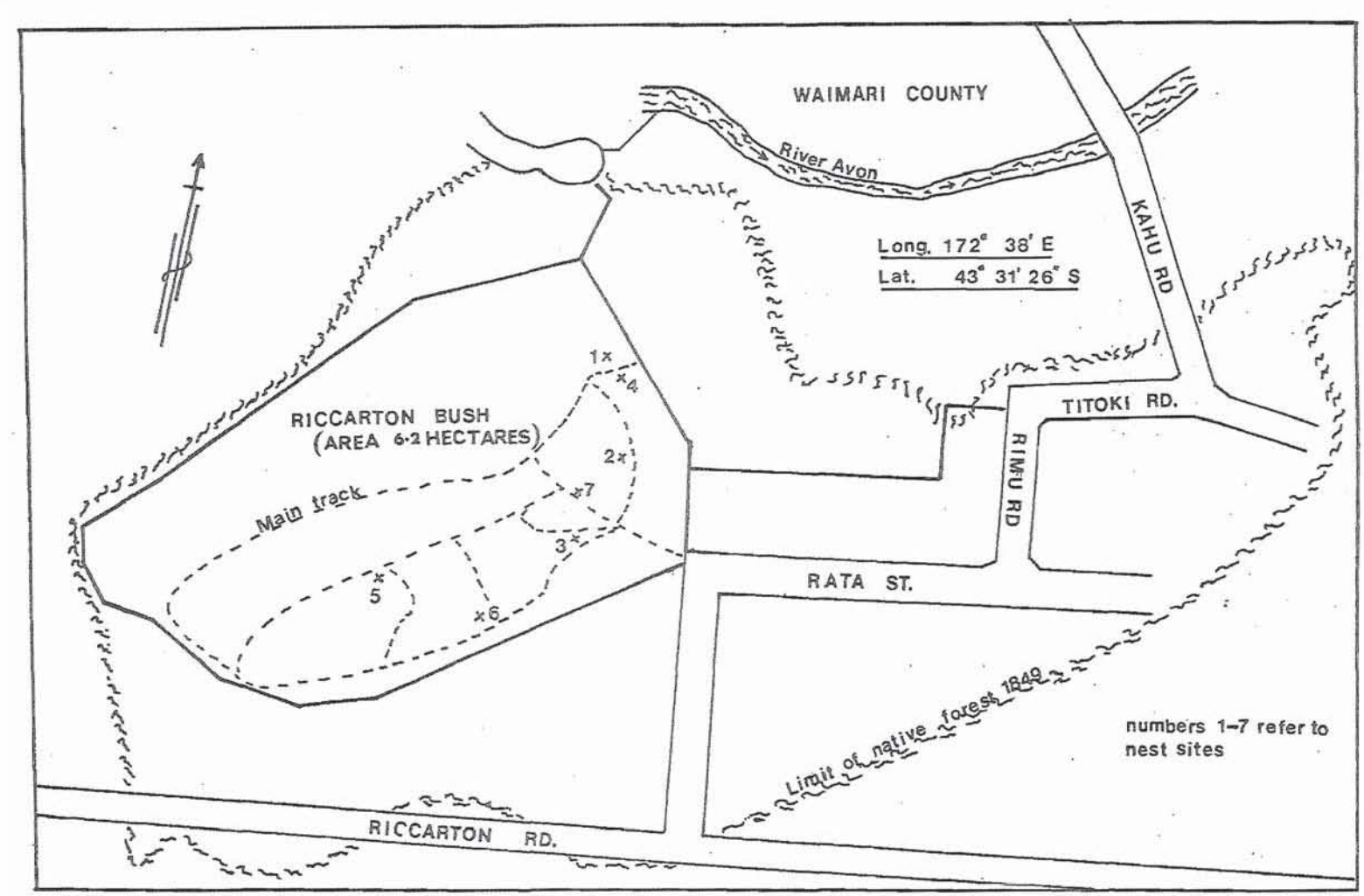


FIGURE 1. Riccarton Bush.

several feet in diameter and rising perpendicularly to a height of 27 to 36 metres, with the lowest branchees some 18 metres from the ground. The Black Pine, or Matai, is not as large as the White Pine and is present in smaller numbers. Growing to nearly the same height as the pines are two other species of trees, the Pokaka *(Elaeocarpus hookerianus)* and the Hinau *(E. dentatus)*.

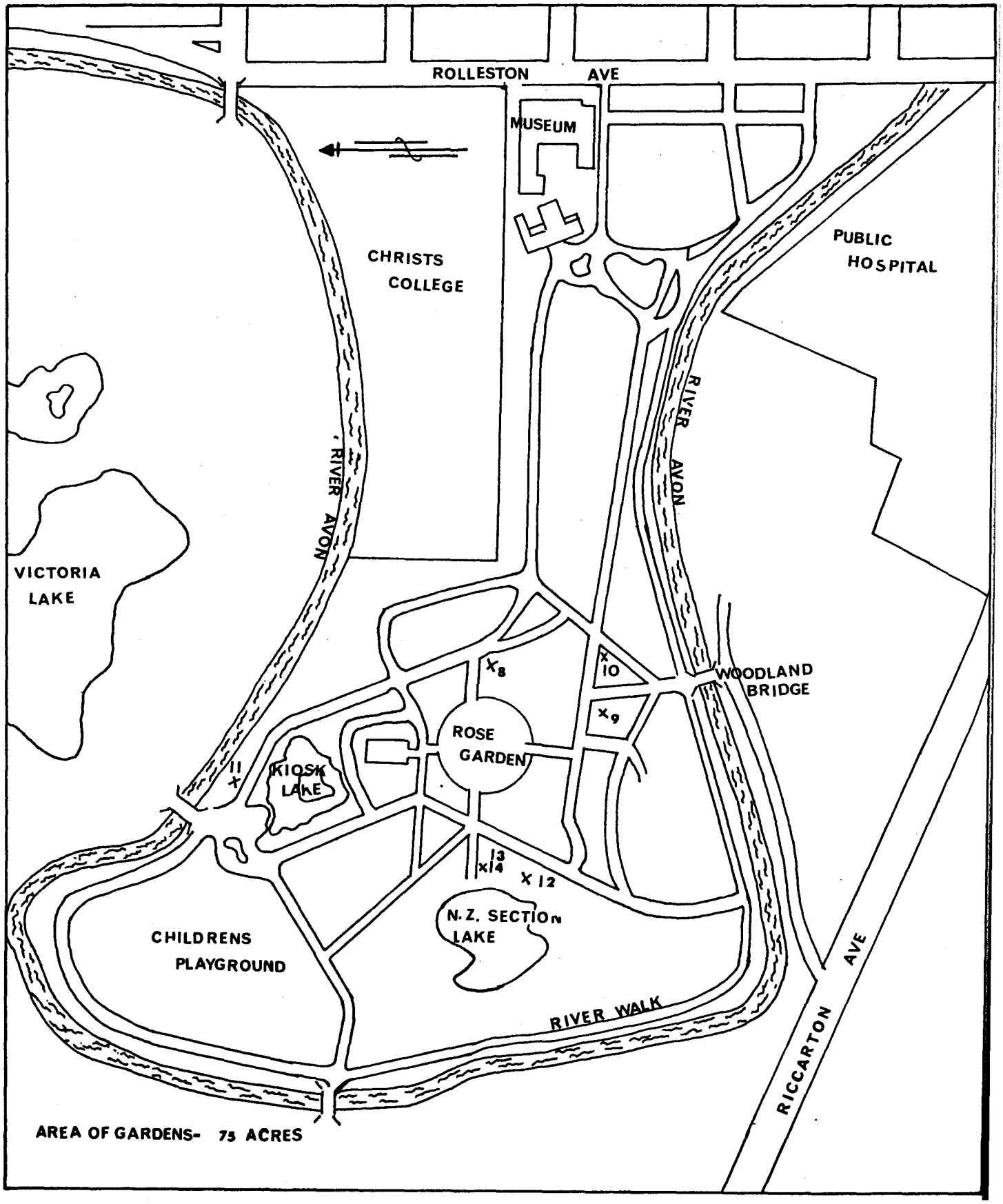
The smaller trees forming the second tier are represented by many more species, *Paratrophis microphylla* (the Milk tree) and *Sophora microphulla* (the Kowhai) being especially abundant.

In the third tier many of the shrubs are young stages of the mature trees, although in most cases the juvenile is so different from the adult that the two forms may be thought to be plants bearing no relation to each other. The juvenile stages of the young Ribbonwood *(Plagianthus betulinus)*, the Kaikonako, the Kowhai, the Pokaka and the Milk tree may be seen bordering many of the paths, often reaching a height of over two metres. The most numerous shrubs are the Wineberry *(Aristotelia serrata)* and various coprosmas.

On the floor of the forest are a certain number of smaller plants and ferns, such typical swamp plants as the Niggerhead *(Carex secta)* and the Toe-toe *(Arundo conspicua)* being among the number. Seedlings of all plants are also found in countless numbers, together with a grass *(Microlaena avenacea)*, forming a living floor of vegetation. Detailed descriptions of the flora of Riccarton Bush are given by Bush (1924), Charles (1950) and "Riccarton Bush Reserve".

A number of well-trodden paths and tracks can be found in Riccarton Bush. Because these tracks have not been mapped, the position of the paths in Figure 1 is only approximate. The nest-sites have been marked on the map.

FIGURE 2. Christchurch Botanical Gardens.



Riccarton Bush abounds with bird life, including both native and introduced species. Among the native birds the fantail, the grey warbler *(Cerygone igata)* and the silvereye *(Zosterops lateralis)* are familiar inhabitants. A native pigeon *(Hemiphaga novaeseelandiae)* was observed twice in Riccarton Bush. The introduced birds inhabiting Riccarton Bush include the House Sparrow *(Passer domesticus)*, song thrush *(Turdus ericetorum)*, the blackbird *(Turdus merula)* and the starling *(Sturnus vulgaris)*. Four species of finches, the greenfinch *(Chloris chloris)*, the goldfinch *(Carduelis carduelis)* and the redpoll *(Carduelis flammea)* are also found in Riccarton Bush.

The opossum *(Trichosaurus vulpecula)*, brown rat *(Mus decumanus)*, and domestic cats were occasionally observed in the bush.

3.4.2 Botanical Gardens

The Christchurch Botanical Gardens cover an area of approximately 75 acres. The Botanical Gardens, with its numerous spacious lawns, is surrounded on three sides by a river. Although many visitors come to admire the various garden features, i.e., the rose garden, azalea garden, rock garden and daffodil woodland, the major feature of the gardens includes the New Zealand plant section and the large collection of exotic trees and shrubs.

In the New Zealand plant section large specimens of the Black beech *(Nothofagus solandri)* and the Red beech *(N. fusca)* are the principal shade trees, with some almost equally-large Ribbonwood *Plagianthus betulinus)* and somewhat smaller houhere. Of the other forest trees the rimu *(Dacrydium cupressinum)*, White Pine and Matai are all represented by comparatively young specimens. A list and description of the numerous plant species in the New Zealand plant section is given by Barnett *et al.* (1968).

The large collection of exotic plants include many species of

Cedar, Conifers, Cypress, Rhododendron, Maples and Gums.

The same species of native and introduced birds which inhabit Riccarton Bush are also found in the Botanical Gardens.

CHAPTER 3

CHAPTER 3

BEHAVIOUR PATTERNS THROUGHOUT THE YEAR

3.1 INTRODUCTION

In this chapter an outline is given of the patterns of behaviour observed during 12 months. A detailed description and discussion of specific aspects forms the basis for Chapters four to twelve.

3.2 METHODS

Observations made each month were analysed for general trends in behaviour.

Observations from March to June (1975) were made of approximately 20 birds, but during the winter months (June to August) this decreased to an estimated eight birds. By August only two pairs were located in Riccarton Bush but another two pairs were found in Hagley Park. From January to March (1976) a population totalling approximately 30 birds (from both localities) was observed.

3.3 RESULTS

3.3.1 March 1975

The fantails were often observed following each other to feed in small groups in the middle storey. There were very few flights, chases, or bouts of "Type 2" vocalisations. Singing and "Type 1" calls occurred but no one type of vocalisation appeared to dominate in March. No moulting was observed.

3.3.2 April 1975

Although the birds were still seen in pairs or small groups there was an obvious increase in aggressiveness between them, with many fights, chases and bouts of aggressive vocalisations. The birds rarely fed quietly together.

3.3.3 May 1975

Very few observations of fantails feeding together were recorded. An increase in feeding associations with silvereyes was noted (Section 9.3.3). "Type 3" vocalisations (i.e., song) characterised this period and were probably due to the setting up and advertisement of winter territories. By May, birds were frequently located in their specific areas of the bush.

3.3.4 June 1975

The number of fantails seen, during June, dropped drastically. Forty-five minutes per hour were spent observing birds during the post-breeding season (January to March) but this was reduced to approximately 10 min/h in June. More time was spent trying to find birds (Section 3.4).

3.3.5 July 1975

The situation in July was much the same as for June. An increase in ground-feeding (Section 9.3) and associations with silvereyes was apparent.

3.3.6 August 1975

At the beginning of August several birds were frequently seen in the canopy, six to 15 metres, continuously singing and occasionally chasing each other. Most observations were made in the same area which was later identified as a territorial boundary between two breeding pairs. The burst of activity was probably associated with the setting

TABLE 1. The timing of events in the breeding cycle.

Pair	Nest	Building begun	Last day of building	Incubation began	Eggs hatched (or day before desertion)	Last day of brooding	Fledged	Deserted
P1R	1	14/8/75*	3/10/75	—	—	—		✓
P1R	2	5/10/75	15/10/75	16/10/75	22/10/75	—		✓
P1R	3	22/10/75	30/10/75	3/11/75	15/11/75	—		✓
P1R	4	17/11/75	20/11/75	21/11/75	6-7/12/75	21/12/75	22/10/75	x
P2R	5	12/ 8 /75	8/9/75	9/9/75	24-25/9/75	7/10/75		✓
P2R	6	10/10/75	13/10/75	15/10/75	30-31/10/75	7/11/75		✓
P2R	7	10/11/75	12/11/75	14/11/75	29-30/11/75	14/12/75	15/12/75	x
P1B	8	10/8/75	18/8/75					-
P1B	9	22/8/75	26/8/75					-
P1B	10	1/9/75	4/9/75	6/9/75	21-22/9/75	7/10/75		x
P1B	11	?						-
P2B	12	?						-
P2B	13	16/10/75	18/10/75	19/10/75	2-3/11/75	18/11/75		x
P2B	14	21/10/75	21/10/75	25/11/75	8-9/12/75	24/12/75		x

* 14/8/75 refers to 14 August 1975.

up of breeding territories. By 7 August, birds were observed in pairs occasionally chasing but mainly following and "Courtship feeding". An increase in "Type 1" calls occurred (Section 10.3.1) and sexual pursuits, nest-site selection and nest-building began.

3.3.7 September to December 1975

The pattern of behaviour for four pairs during the breeding season is given in Table 1 and Figure 3.

The general pattern for each pair was:-

(i) nest-site selection (Section 5.3.2),

(ii) nest-building (Section 5.3.5),

(iii) courtship. Although courtship occurred throughout the nest-building period there were usually one or two days before egg laying and incubation, during which large numbers of courtship displays and copulatory acts were seen (Section 4.3),

(iv) incubation. This usually lasted 13 to 14 days (Section 6.3),

(v) nestling which lasted 14 to 15 days, and

(vi) post-fledging. After the young fledged the parents spent several days feeding them before starting a new nest. They continued feeding during nest-building and the start of incubation (Section 7.3.5).

One pair had three broods in succession but the others had one or two, deserting other nests at various stages in the breeding cycle. Blackburn (1965) noted that three broods during one season were common.

3.3.8 January 1976

A few observations of parents feeding fledglings were made in January, this being now the end of the breeding season.

Independent fledglings frequently fed in groups of six to eight. They resembled the adults in size and dimensions. The eyebrows and wing

bars were orange compared with the white of their parents. Stead (1932) also noticed this feature in young fantails. The fledglings' chest feathers were mottled with orange, and black juveniles had a distinct orange tinge. These differences were only obvious on close inspection and juveniles could not be distinguished from parents at a distance.

The adults showed signs of moulting. All birds undergoing tail moult had replaced the central feathers first, while the outer rectrices were usually broken and untidy. These birds did not allow me to approach closer than three to five metres and never approached me as they had earlier in the season. The juveniles frequently approached and stayed around me at this time. They appeared to be extremely curious.

3.3.9 February 1976

Observations made in February were similar to those in January. The fantails frequently fed in groups or in pairs.

3.4 DISCUSSION

A detailed discussion on the annual pattern of the behaviour of the South Island Fantail is difficult to make on the basis of a single 12 month study. Discussion on specific aspects is given in the following chapters. Because of the obvious decrease in the population size over the winter months, a further discussion on this aspect is warranted. There are three possible causes for the decrease in birds observed:-

(i) the birds were difficult to locate because of a marked decrease in calling and singing (Section 11.3.2),

(ii) winter mortality. Although information of survival rates in the New Zealand Fantails is not available, a 12 year study on the Pied Fantail Flycatcher *Rhipiduia javanica* (McClure 1974)

showed a two-thirds loss of population in the first year followed by a slow loss to 4.5% survival past nine years. It is possible that such a high mortality of juveniles also occurs in the South Island Fantail, and

(iii) seasonal migration. Although no information is published for the New Zealand Fantail on this aspect, the Australian Grey Fantail undertakes an "apparent regular seasonal movement, a partial exodus from its Southern range in winter" (Slater 1975). The Willie Wagtail and the Rufous Fantail *Rhipidura rufifrons* also migrate long distances. It is very likely that the New Zealand Fantail exhibits seasonal migration. I have noticed an increase in the number of fantails in the residential areas of Christchurch between March and May each year. The birds concentrate in suitable breeding areas, i.e. local native reserves and parks during the summer and are not frequently seen in the suburbs or residential areas until March. At this time I am constantly informed of the presence of fantails around friends' and neighbours' homes. It is difficult to know whether this is an indication of migration, or merely a displacement of juveniles out of parental territories. A detailed study of this aspect would be warranted.

CHAPTER 4

CHAPTER 4

THE DISPLAYS OF THE SOUTH ISLAND FANTAIL

4.1 INTRODUCTION

"The word display, as used in the study of behaviour, means the showing off of certain actions or the making of sounds innate and common to the species. Display communicates to mate, species member, or-rarely-other species members, the instinctive intentions or state of the bird and causes proper instinctive responses" (Darling 1963).

Although there have been many studies of passerines involving the interpretation of displays (Van Tets 1965, Marler and Hamilton 1966, Hinde 1970, Morris 1970), the origin of display components (Andrew 1961), the nature of hostile displays (Moynihan 1955), and ritualisation of intention movements (Daanje 1950), there is very little information on these aspects in any species of *Rhipidura*. Only one description of a display (Hough 1969) by a species of Muscicapinae or Rhipidurinae was found in my literature search.

In this chapter a detailed description of the displays of the South Island Fantail is given. Information on the presence or absence of "Tail fanning" and "Tail flicking" during these displays is included. In other passerines "Tail fanning" and "Tail flicking" are components of courtship (Hinde 1955, Davis 1958) and aggressive displays (Von Haartman 1956).

In each section notes on releasing stimuli are made. However, it should be borne in mind that because of unknown variables, particularly physiological states, these stimuli do not always elicit a response.

4.2 METHODS

Descriptions of the displays of the South Island Fantail are based on field observations of four pairs. Individuals were identified by previously placed paint markings or individual differences in plumage. Observations were made in the nest-site when the birds were within 8.5 m of me. I had great difficulty photographing and obtaining cinematographic information of the displays but hope to obtain photographic evidence of these displays in the very near future.

4.3 RESULTS

4.3.1 Pre-fertilisation Displays

Pre-fertilisation displays include "besides the aggressive behaviour involved in the establishment of territories, the activities that serve to bring the sexes together and, in many species to form and maintain the pair-bond" (Pettingill 1970). A number of pre-fertilisation displays including "Sexual pursuit", which refers to the non-aggressive pursuit of a female by the male through the air (Pettingill 1970), and "Courtship feeding", which involves the feeding of one member of an adult pair by the other (Thomson 1964), were identified in this study.

4.3.1a "Sexual pursuit"

"Sexual pursuit" in the fantail occurred during pair-formation, nest-site selection and nest-building. The male frequently followed the female to and from the nest or through the bush. To the female "Sexual pursuit" probably indicates the male's readiness to copulate.

4.3.1b "Courtship feeding"

Feeding of the female by the male occurred frequently (as many as 30 times/hour) during pair formation and nest-building but ceased once incubation began. "Courtship feeding" interrupted the female's foraging

activities and collection of nest-material at the beginning of the nest-building period, but during the later stages she spent less time foraging, collecting nest-material and building and more time following the male. She chased few insects, in contrast to the male who fed actively.

After capturing the prey, the male made fast direct flights (two to eight metres) to his mate, who was located by sight or by the calls she gave when collecting nest-material. If the female was not found he proceeded to the nest, pivoted below it, and gave the "Feeding vocalisation" (Section 11.3.1). The female usually responded by approaching or calling from her position in the canopy. If she did not, the male swallowed the insect. The fact that the male often seeks out his mate suggests that he is capable of initiating the behaviour without any apparent signal from her.

On landing near the female, the male usually positioned himself (w.r.t. her) in one of three ways:

(i) parallel. The pair stood close together across the branch. The male turned his head to feed her. Forty-two per cent of 163 observations were of this form (Table 2),

(ii) right-angles. The male's body was in line with the branch and at right-angles to the female. It accounted for 37% of the observations, and

(iii) head-on. The two birds stood facing each other during 21% of the observations.

There was a significant difference ($\chi^2 = 111$, df = 1, $p > 0.001$) between "Head-on" orientations and the other types of orientations during "Courtship feeding".

A "Head-on" orientation is an aggressive component of displays between most passerines during the non-breeding season and rival males in the breeding season.

TABLE 2. The orientation of the male's body with respect to the female during "Courtship feeding".

Body orientation	Number of observations	Percentage frequency of observations
Parallel	68	42
Right-angles	61	37
Head-on	34	21
Totals	163	100

The frequent occurrence of this component in my observations of "Courtship feeding" may be due to the fact that the aggressive nature of the orientation does not completely disappear (between the pair) once breeding begins.

The female often hopped away as the male approached her, probably reflecting a weak pair bond. The male usually followed for several centimetres, then attempted to feed her as she assumed a submissive posture, i.e., body crouched and head lowered to a position in line with the body, tail closed and wings held close to the body. When she gaped, very bright yellow markings in the buccal cavity were visible. The male's dominant posture was characterised by an upright body and downward pointing bill. The tail was slightly fanned and held 45° to 60° above the horizontal position. "Courtship feeding" was not accompanied by "Wing shivering" in the fantail; a common component of "Courtship feeding" in many passerine species (Andrew 1961).

Most "Courtship feeding" involved the presentation of large insects, which were subsequently subdued (i.e., knocked or pecked) by the female. On some occasions there appeared to be no transfer of food. It is possible that the South Island Fantail engages in "Symbolic courtship feeding", but small insects or regurgitated food that I could not see may have accounted for the apparent absence of food during the

exchange.

After feeding, the male's tail fanned open as he turned to "Bill-wipe" or move through the branches. The female also "Bill-wiped" before continuing her activities (i.e., preening, resting, foraging or nest-building). Copulation followed "Courtship feeding" on only two occasions. Other displays associated with "Courtship feeding" included "Hop-over" and "Head-swaying" (Table 3).

TABLE 3. Displays associated with "Courtship feeding"

Displays	Number of observations	Percentage frequency of observations
"Courtship feeding" only	282	98
"Hop-over" after "Courtship feeding"	1	0.5
"Hop-over" before "Courtship feeding"	2	0.5
"Head-swaying"	3	1
Totals	288	100

"Courtship feeding" occurred on the ground and in all parts of the canopy, but "Aerial Courtship feeding" observed by Blackburn (1965) and Soper (1972) was observed in only 1% of 288 observations.

4.3.1c "Body-contact" Display

A fantail hopped sideways to bump into the side of its partner and remained 'clumped' for one to four seconds during the "Body-contact" display. The bird performed a "Hop-over" display (Section 4.3.1d) after the contact in 37% of 35 observations, but usually moved away and either:-

(i) turned on the perch to sit facing away from the mate, or

(ii) flew away.

On approach and contact neither's tail was fanned, the body was in a normal posture, and no vocalisations were given. The bird that was approached sat motionless.

The display was performed by both sexes during nest-site selection and nest-building. The "Body-contact" display occurred on the branches and occasionally on the nest. The male often landed in the nest and pushed up against the female, who stopped building for several seconds before the male moved out or "Hopped-over" her (Table 3).

4.3.1d "Hop-over" Display

The "Hop-over" display included the following elements:-

(i) an initial approach,

(ii) an orientation of the displayer's body, parallel or right angles, with respect to that of its mate, and

(iii) a hop over the back of the partner, who stood motionless.

Occasionally the bird landed momentarily on the back of its mate during the hop.

In 23% of 56 observations the "Hop-over" was preceded by a "Body-contact" display.

After a single "Hop-over" one of the following activities occurred:-

(i) the recipient of the display flew away,

(ii) the displayer hopped along the branch a few centimetres and sat singing, preening or resting,

(iii) the displayer repeated the display several times,

(iv) the displayer flew away, or

(v) there was a bout of "Hop-over" displays involving both birds.

The display was rarely followed by copulation.

The recipient stood rigid with head lowered and in line with the body during the approach and hop. The bird never directed its head

towards the mate, who approached with a tightly closed tail held in line with the body.

The display was incorporated in nest-site selection and occurred during nest-building. The selection of Nest 1 was accompanied by many flights to, and up under Cabbage Tree *(Cordyline australis)* fronds (one of which was selected as the nest-site) where the bird stood and called. The display occasionally occurred in the nest (while building) but mainly on the branches of trees in the pair's territory.

On many occasions the parent performed the display before feeding fledglings who were also observed "Hopping-over" siblings.

The display was given by both sexes.

4.3.2 Fertilisation Displays

Fertilisation displays are those displays directly associated with copulation. Fertilisation displays include precopulatory displays, copulatory displays, i.e., "the movements of both sexes from the time the male mounts the female until coition is effected and the male dismounts" (Pettingill 1970) and postcopulatory displays. Postcopulatory displays, which take place immediately after the male dismounts, were not identified in the South Island Fantail.

4.3.2a Precopulatory Displays

In the fantail a precopulatory display by the female preceded 81% of the 31 copulation attempts and included the following components:-

(i) an initial orientation of the female's body towards the male,

(ii) a large number of high pitched calls, given in rapid succession,

(iii) flexed legs,

(iv) a lowering of the body in the horizontal plane,

(v) a slight upward pointing of the bill,

(vi) a closed tail, held 45° above the body axis, and

(vii) vibration of the wings, which were held well above the back and

TABLE 4. A summary of the behaviour associated with the male's displays.

Recipient of the display	Associated behaviour 1.	Associated vocalisation 2.	The female's behaviour prior to the display	The female's subsequent behaviour	Stage of the breeding cycle 3.	Major functions of the display
Female	Flight	"Type 1"	Flight past the male. Flight of the female to the nest.	Land on a nearby tree. Continuation of her flight.	Pair-bond formation. Nest-building. Incubation.	Formation of the pair-bond. Sex recognition.
Female	Flight to the female. Pivot. Bill-wipe.	"Feeding vocalisation"	Following the male. Foraging. Nest-building. Collecting nest material.	Bill-wipe. Forage. Nest-building.	Pair-bond formation. Nest-building.	Maintain and strengthen the pair-bond.
Female	Foraging. Nest-building.	None	Sitting, resting or preening. Nest-building.	Continuation of nest-building or other activities.	Pair-bond formation. Nest-building.	Pair-bond formation.
Female Fledglings	Foraging. Nest-building.	None	Sitting, resting or preening. Nest-building.	Continuation of nest-building or other activities.	Pair-bond. Nest-building. Care of fledglings.	Pair-bond. Family-bond.
Female	Approach to the nest. "Aerial feeding".	"Type 1"	Sitting on nest. Incubating or brooding.	Flight out of the nest.	Incubation. Brooding.	Signals the male's readiness to relieve the female on the nest.
Female Rival Silvereye Song Thrush	Chase or attack. Threat	"Type 2" "Type 3" "Fast type 1"	Flight past the male calling "Fast type 1". Close proximity of the other passerines to the nest.	Continuation of the flight.	Throughout the breeding season.	Threat.
Female	Attempt to "Courtship feed" or copulate.	"Type 2"	Flight past the male. Aggressive call. Song.	Submissive display. Flight away from the male.	Nest-building.	Threat.
Rivals	Tail "whipping" Jump towards the opponent.	"Type 2" "Fast type 1"	Close proximity between the birds.	Submissive posture.	Throughout the breeding season.	Threat.
Rival male. and occasionally females.	Tail "whipping". Jump towards the opponent.	"Type 2" "Fast type 1"	Close proximity between the birds. Submissive posture.	Submissive posture.	Throughout the breeding season.	Threat.

s behaviour exhibited by the male either simultaneously or immediately before or after the
haviour.

the acoustic signal accompanying the behaviour.

hen in the breeding cycle the behaviour was most frequent, although some observations
:curred throughout the cycle.

slightly spread. The wing vibration differed from that given in an aggressive context in that:-

a) the wings were not fully extended,

b) the wings were bent at the carpal joints,

c) the amplitudes of the vibrations were greater, and

d) the frequencies of the vibrations were smaller.

The precopulatory display was given on perches in the nest-site during pair-formation and nest-building.

4.3.2b Copulatory Displays

The male fantail responded to the female's song and precopulatory display by approaching and orientating himself parallel to her. As the male mounted, her wing vibrations ceased, although her wings remained raised, her body lowered, and tail closed, laterally displaced and held in a horizontal position. The male stood on the female's back in a more upright posture, while his tail was placed to the side of, and below, the female's. The male's tail was closed most of the time but fanned open for a few seconds before dismounting. This was probably the instant of coition.

Although the male's balance was aided by the rotation of his wings throughout the display, he frequently fell off, and occasionally responded by performing a "Head-swaying" display below her (Table 4).

After coition the female usually flew away.

4.3.3 Post-fertilisation Display

Post-fertilisation displays occur after egg-laying, and acts to strengthen the pair-bond and facilitate parental behaviour. The most frequent type of Post-fertilisation display in passerines is the "Nest-relief" display. Male and female fantails frequently performed an "Aerial nest-relieving" display during incubation and brooding.

The display incorporated a large amount of aerial acrobatics above or in front of the nest during nest-relief. If the bird on duty did not fly off, the displayer returned to a perch nearby and repeated the display. These activities made the relieving bird very conspicuous.

4.3.4 Hostile Displays

Hostile activities include attack and escape movements of very different intensities, plus a large number of more complex reactions. The most widespread, frequent and conspicuous of these complex reactions are "ritualised" patterns or displays; patterns that have become standardised and specialised as social signals or releasers (Moynhan 1955). Hostile activities are common components of the male courtship display, the female precopulatory display, and "Courtship feeding" in many passerines (Andrew 1961), and include "Wing-shivering", threat and submissive postures. Another Hostile display, the "Head-swaying" display, was identified in the South Island Fantail.

4.3.4a "Wing-shivering" Display

In this study "Wing-shivering" occurred during:-

(i) a few encounters between members of a pair at the beginning of the breeding season. The male sometimes displayed as the female sang, gave aggressive vocalisations from the nest, or flew past him without prior warning (i.e., calling). When both birds flew towards the nest at the same time, one bird stopped short and directed the "Wing-shivering" display towards the male in 80% of the 45 observations (Table 5),

(ii) attacks on the silvereye and thrush during the breeding season. Although 18% of 46 "Wing-shivering" displays were directed towards these passerines, there was a significant difference ($\chi^2 = 36$, df = 1, $p > 0.001$) in "Wing-shivering" towards other fantails and other passerines, and

(iii) occasionally during "Courtship feeding" and after copulation (Table 5).

TABLE 5. Behaviour associated with "Wing-shivering"

Behaviour associated with the "Wing-shivering" display	Number of observations	Percentage frequency of observations
During encounters with partners	36	80
During attacks on other passerines	8	18
During "Courtship-feeding"	1	1
After copulation	1	1
Total	46	100

The components of the "Wing-shivering" display included leg flexion and a lowering of the body, while the wings were raised, spread and vibrated rapidly. The amplitude of these movements was very small in that the wings were never raised above the level of the back or lowered below the chest. The tail was closed and held in line with the body as the bird faced and pointed its bill toward the opponent.

4.3.4b "Head-swaying" Display

The "Head-swaying" display, observed 31 times during the later stages of nest-building, was a peculiarity of the male. In this study it was always directed at the female, and included the following components:-

(i) sleeked body,

(ii) wings held well back and close to the body,

(iii) legs extended,

(iv) bill raised and pointed at the female (who was usually above the male), and

(v) movement of the head from side-to-side as the neck was stretched.

The female responded by crouching with head lowered, tail tighly closed and raised to a vertical position. Her body feathers were usually ruffled.

The display was given after the female:-

(i) sang near the nest,

(ii) "Wing-shivered" at the male, and

(iii) chased the male when he approached her.

He occasionally "Head-swayed" after falling off the female (during copulation).

The male usually stopped as the female turned and "Waltzed" away. However, the display was once followed by copulation and twice by "Courtship feeding" (Table 6).

TABLE 6. Behaviour after the "Head-swaying" display

Behaviour pattern	Number of observations	Percentage frequency of observations
Separation of pair	28	90
Copulation	1	3
"Courtship feeding"	2	7
Total	31	100

4.3.4c Threat Postures

Twenty-eight instances of threat displays were observed during encounters between rivals and included two main components:-

(i) pivoting. This involved rapid lateral body swinging as the bird stood on one spot. The frequency of turns resulted in a "Whipping" of the closed tail from side-to-side. The body was lowered to a horizontal position as the bird faced its opponent. Although pivoting was also associated with feeding behaviour, the

frequency of turning was smaller in that context, and

(ii) bill-lowering. The body and head were lowered to a horizontal position and directed towards the oponent. The tail was closed and in line with the body. Unlike Carduelinae, which exhibit a similar display (Andrew 1961), the bird did not gape and the wings were not raised. It is likely that other components, not detected by me, were used in threat displays. Willie Wagtails show aggression simply by expanding their eyebrows (Hough 1969, Ives 1975), a characteristic of displays by the South Island Robin *Petroica australis* (Flack 1976). Eyebrow "flashing" was not readily observable in fantails but may be detected with the aid of cinematography.

4.3.4d Submissive Postures

I observed submissive postures four times between mates and ten times between rivals (i.e., neighbours). The posture consisted of perching (slightly crouched) with head withdrawn and body feathers raised. The subordinate individual usually faced away from the aggressor.

4.4 DISCUSSION

Most of the displays of the South Island Fantail are similar to those given by many species of passerines.

Although "Courtship feeding" is common in many groups of birds the roles of the sexes and the manner and significance of feeding differ markedly. In nearly all birds it is the male which feeds the female (Lack 1940). Lack (1940) believes that the reason the male should give the food and the female receive it, and not the reverse, is far from clear. The reason for this behaviour in the South Island Fantail, and probably a number of other passerines, could be connected with the

different roles the sexes play in nest-building. In the fantail the female does most of the building and spends little time feeding, unlike the male who continuously feeds and follows the female. Therefore, the contribution from the male probably helps provide her with the energy required for maintenance activities and egg-development at a stage at which she has little time to feed herself. "Courtship feeding" in the fantail may also function in maintaining and strengthening the pair bond, as a result of a decrease in aggressiveness due to habituation to the mate's proximity. Feeding was not associated with copulation, as it appears to be in some passerines. "Courtship feeding" probably ceased once incubation began (Section 4.3.1b) because the parents shared incubation equally, both having the opportunity to feed in between incubation spells.

I could not find any reference to a similar "Body-contact" display by any other species of passerine. In this study the display was given by fledglings and adults and appeared to function in group and pair maintenance as a result of a close proximity between individuals. The body-contact differed markedly from thermoregulatory clumping, in that it was of extremely short duration. Although roosting behaviour in adults was not observed I doubt whether this display could be confused with thermoregulatory behaviour in adults as the duration of contact was too short to have energy-saving benefits.

Unlike the "Body-contact" display, the "Hop-over" display has been noted in a number of passerines. A similar display in the Willie Wagtail was described by Hough (1969); "while she remained in the one spot, he cart-wheeled continuously from one side of her to the other, over and in front of her, landing on the branch about 15 to 25 centimetres on each side and sometimes swinging under it". The display in the fantail probably functions in maintaining and strengthening both

pair and family bonds. It was not associated with copulation.

The components of the female fantails' precopulatory display also resembled those precopulatory displays of other passerines, i.e., sleeked body feathers, "Wing-shivering" and crouching. These components suggest a submissive role by the female (Pettingill 1970). Among many passerines the males perform a precopulatory display, in which their body feathers are ruffled, the wings are spread, the tail is lowered and spread, while the bird bows (Pettingill 1970). I did not observe such a display in the fantail. This could be due to the fact that copulation was initiated by the female, i.e., as soon as the female exhibited a precopulatory display the male approached and mounted her. The absence of vertical tail vibration during the precopulatory display correlates with its absence in other species of Muscicapinae (Andrew 1961).

The "Wing-shivering" display has been observed and described in many groups of birds. In many passerines "Wing-shivering" is a common component of the male courtship display, the female precopulatory display and "Courtship feeding". It is also used in reproductive fighting in some species (Andrew 1961), the best known local example being the silvereye. The fact that "Wing-shivering" was not given before copulation, rarely observed during "Courtship feeding" and was frequently a component of aggressive encounters (Table 4) incorporating attack (i.e., bill-lowering, bill-pointing and sleeked feathers) and flight intention movements (i.e., crouching and spreading wings), suggests that it is a hostile display "designed" to intimidate an opponent, to make the opponent retreat or flee. The "Head-swaying" display also incorporated attack (i.e., bill-pointing and sleeked body) and submissive components (i.e., a positioning below the female). It appeared to be used to threaten the female.

"Tail fanning", "Vertical tail flicking" and "Tail flashing" (Sections 12.2, 12.3, 12.4) were not observed in any of the courtship displays, and although tail fanning and flicking are components of hostile and aggressive displays of some passerines (Von Haartman 1956, Andrew 1961) they were not evident in the displays of the South Island Fantail.

CHAPTER 5

CHAPTER 5

NEST-BUILDING BEHAVIOUR

5.1 INTRODUCTION

Nest-building behaviour is defined as "that behaviour concerned with excavation or construction of nests" and includes nest site selection, collection of material and the actual construction of the nest (Thomson 1964).

5.2 METHODS

The building of 12 nests by four pairs of birds was studied. Because most nests were built high in the middlestorey and could not be removed, a detailed description of nest structure was not possible.

A number of standard observations on nest-building were made during two to three hour periods at the nest. The standard observations included:-

(i) the sex of the bird entering the nest,

(ii) building techniques. The building movement used on entering and before leaving was noted. The number and position of "Body-presses" (Section 5.3.6) in the nest were recorded,

(iii) time spent building,

(iv) the behaviour:-

a) as the bird left the nest,

b) while off the nest. The birds collected the material 0.5 m to 9 m away, and were observed most of the time from my position near the nest,

TABLE 7. Nest sites.

Location of nest	Nest	Date of nest-building	Height of the nest above the ground (metres)	The genus or species of the tree in which the nests were found
Riccarton Bush	1	14/8/75	6.0	*Cordyline australis*
Riccarton Bush	2	5/10/75	5.0	*Coprosma*
Riccarton Bush	3	22/10/75	2.5	*Hoheria*
Riccarton Bush	4	17/11/75	9.0	*Pittosporum tenuifolium*
Riccarton Bush	5	12/8/75	2.1	*Cordyline australis*
Riccarton Bush	6	10/10/75	3.0	*Myrsine australis*
Riccarton Bush	7	10/11/75	2.4	*Melicytus ramiflorus*
Botanical Gardens	8	10/8/75	3.6	*Cupressus macrocarpa*
Botanical Gardens	9	22/8/75	2.1	*Dacrydium cupressinum*
Botanical Gardens	10	1/9/75	1.5	*Coprosma*
Botanical Gardens	11	—	3.0	*Coprosma*
Botanical Gardens	12	—	2.4	*Dacrydium cupressinum*
Botanical Gardens	13	16/10/75	2.4	*Pseudopanax crassiformes*
Botanical Gardens	14	21/10/75	2.4	*Pseudopanax crassiformes*
Kowhai Bush	15	—	1.8	*Leptospermum ericoides*
Kowhai Bush	16	—	2.4	*Coprosma*
Kowhai Bush	17	—	1.8	*Melicytus ramiflorus*
Kowhai Bush	18	—	2.0	*Coprosma*
Kowhai Bush	19	—	11.0	

c) as the fantail approached the nest,

(v) the behaviour of the birds when they were close to each other, and

(vi) time spent away from the nest.

Most nests were too high to be removed so detailed information on the nest structure and quantity of nest material was impossible to obtain. The heights of the nests were determined with the aid of a measuring stick marked in half metre lengths.

Seventy-two hours were spent observing nest-building behaviour. Variation in the amount of building from day-to-day was noted in 24 standard two hour periods (between 1100h and 1300h) at several nests. I chose to observe nest-building between 1100h and 1300h after a preliminary investigation revealed a large amount of nest-building activity during this period. Although diagrams on the variation of the amount of nest-building from day-to-day are based on observatios of two pairs, the same trends were noted in other fantails. Time did not permit a detailed quantitative study on this aspect for all birds.

5.3 RESULTS

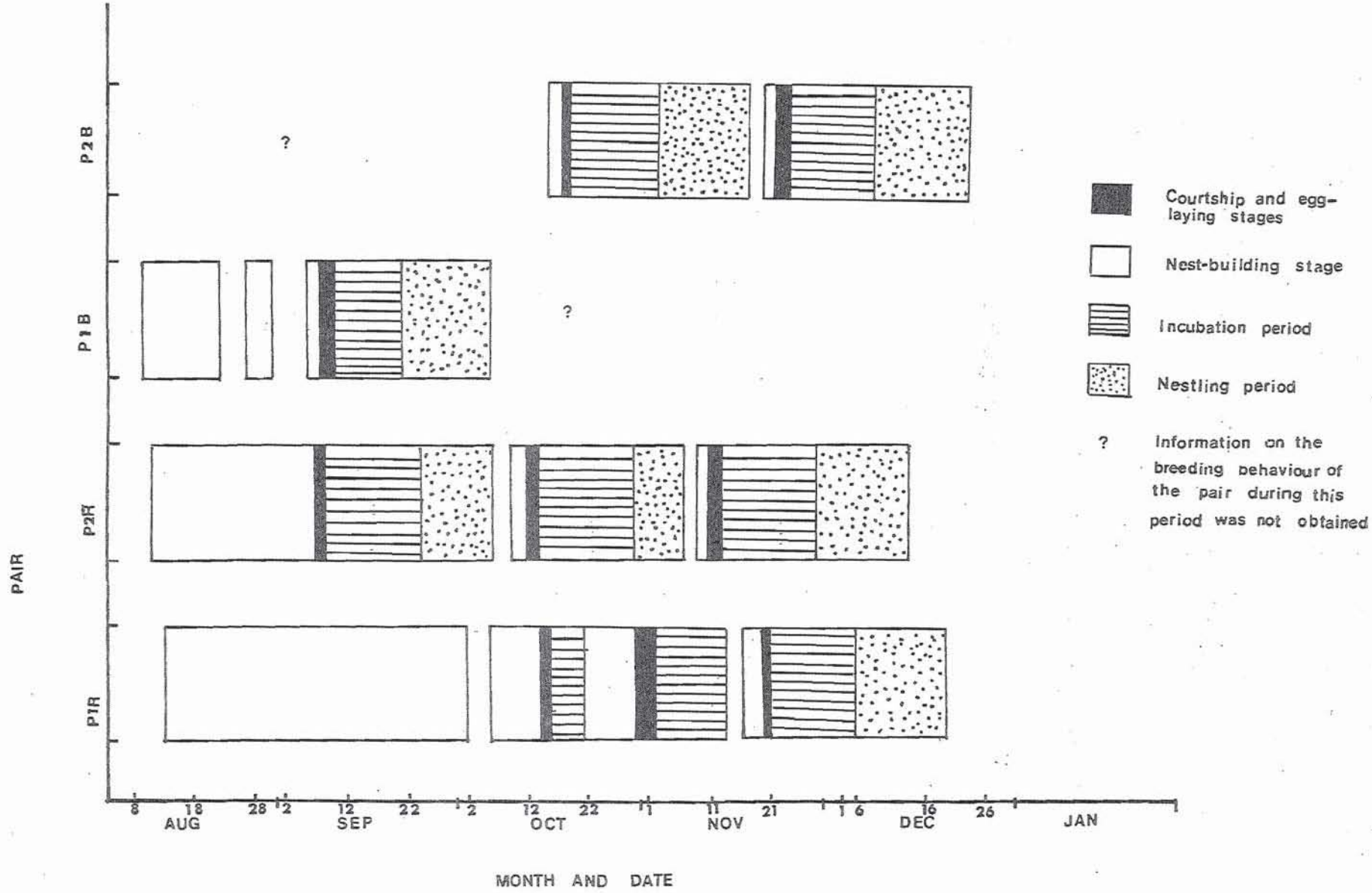
5.3.1 Nest Sites

South Island Fantails nested in native and introduced species of trees, between two and eight metres above the ground (Table 7). All the nests were well concealed in the surrounding vegetation.

5.3.2 Nest Site Selection

I observed the selection of two nest sites, viz. Nest 1 and Nest 6 by P1R and P2R respectively. A description of the behaviour of P1R is as follows. Between the 7 and 14 August 1975, P1R repeatedly flew beneath the inner leaves of one or other of fifteen Cabbage trees,

FIGURE 3. The timing of events in the breeding cycle.



located in its territory. The bird (male or female) gave "Loud Type 1" calls during these flights. The calling attracted the attention of the mate who followed the caller to the tree. "Body-contact" and "Hop-over" displays occurred on the trunk. The pair spent 30 to 60 seconds in the Cabbage tree before either, one flew out while the other remained preening, or, both flew in opposite directions to nearby perches. They preened before foraging or repeating the sequence. Nest-building began in one of these trees on 14 August.

Similar behaviour was observed during the selection of Nest 6 by P2R. The displays occurred in Cabbage trees and a Red Matipo tree *(Myrsine australis)* which was selected as the nest site.

A decrease in the interval between nest site selection and building as the season progressed was recorded for all fantails studied. The selection of the site for Nest 1 began in a warm spell at the end of winter, and building started seven days later (Fig. 3). This differed from the two day interval between the desertion of Nest 1 and Nest 2. The building of Nest 3 and 4 began the day the previous nests were deserted.

5.3.3 Nest Material

The South Island Fantail used material close at hand, such as fine strands of bark, flax and cabbage leaf fibres, very small twigs, dried grass, clumps of rotten wood, moss and cobwebs. Two nests removed from Kowhai Bush contained sheep's wool, probably collected from nearby fences and paddocks.

The South Island Fantails faced the outside of their nests with cobwebs.

5.3.4 Collection of Nest Material

The male and female fantail collected nest material.

Most material was collected from the ground, where the fantails hopped with tail closed and held 60° to 90° above the level of the back. The wings were positioned close to the body but fluttered (probably to aid balance) as the bird bent to pull or pick up the nest material. At the same time the tail flicked forwards and back over the bird's head as a result of the body movements. Other collecting techniques included:-

(i) the detachment of fine pieces of bark or vegetation in branches, by grasping the strand in the bill and pulling with a sideways movement of the head, and

(ii) scraping rotten wood with the bill.

Cobwebs were pecked from webs.

The fantails collected material one half to ten metres from the nest. The birds often rejected some of the material they picked up.

5.3.5 Nest Construction

After selecting nest material the fantails gave "Type 1" calls during direct flights to the nest. The birds often landed on a perch near the nest and continued calling before flying up to build. On completion, the bird flew to a nearby perch, preened its chest and occasionally "Bill-wiped" or "Scratched" before returning to its collection area. The female occasionally gave "Type 1" calls while perched, but never sang. The male often sang after building.

At the start of nest-building the birds alternated visits to the nest, one leaving as the other approached. If a bird failed to leave, its mate waited on a nearby perch or landed on the nest, pushing into the bowl to force the other out.

As nest-building progressed the male tended to follow the female to the nest and stood watching her build. He frequently stopped short and sang or preened below the nest but occasionally built with her, fed her in the nest, performed a "Body-contact" display or "Hopped-over her

(Table 8).

TABLE 8. Behaviour of the male after following the female to the nest.*

Behaviour	Number of observations	Percentage frequency of observations
Stands on rim watching female, follows her off	20	26
Stands on rim, follows female off, then feeds her	14	18
"Hops-over" female in the nest, then leaves	11	14
Does not enter the nest, but preens and sings near it	10	13
Stands on the rim until the female leaves, then builds	9	12
Performs a "Body-contact" display, then leaves	7	9
Builds with the female	3	4
Feeds the female on the nest	2	3
"Wing-shivers" below the nest as she enters	1	1
Total	77	100

* Based on observations of four pairs at 12 nests.

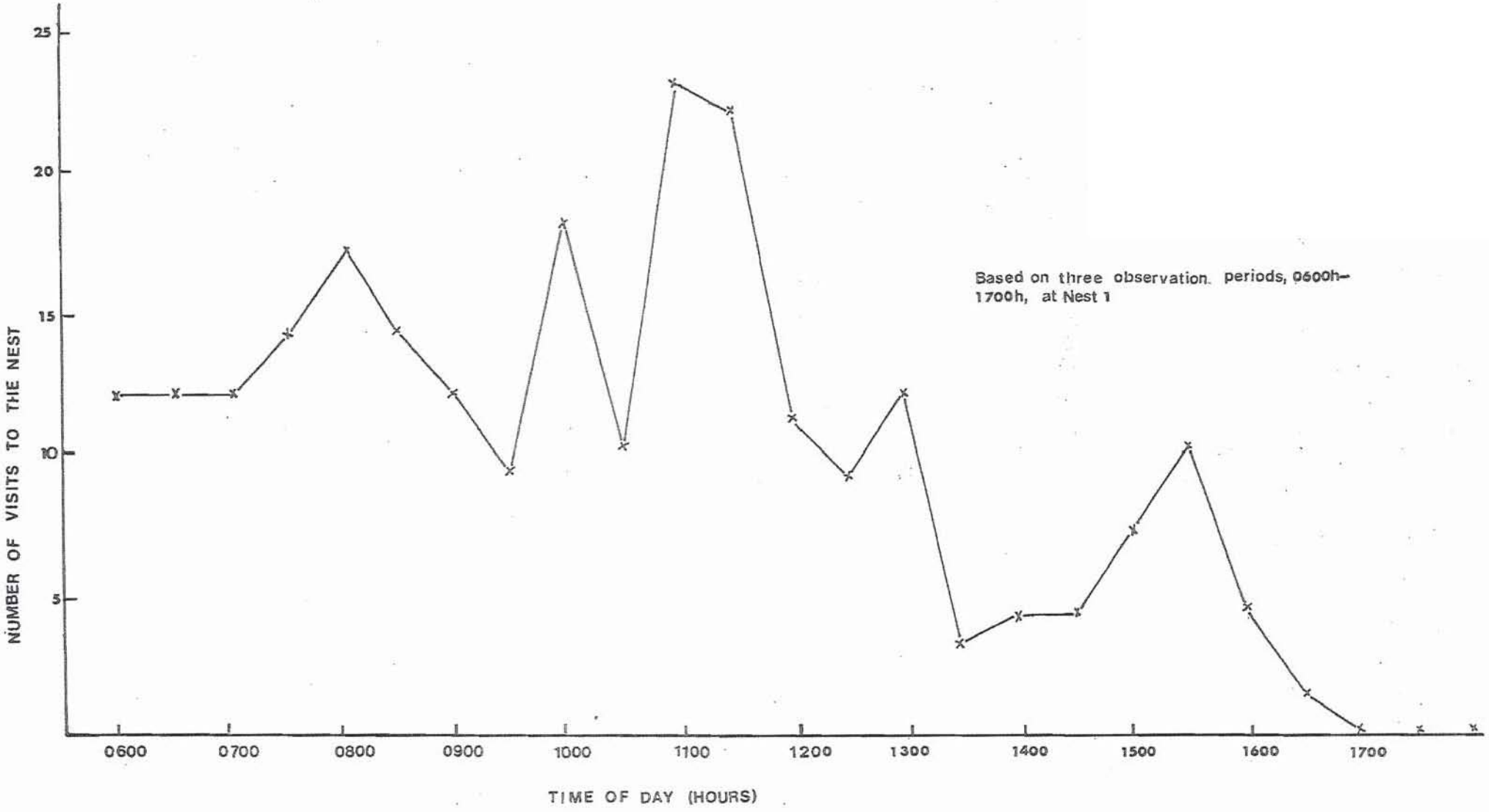
The female appeared to play a greater role in nest-building than the male (Table 9). Not only did she make more visits to the nest but she also spent longer periods building.

TABLE 9. Role of the sexes in nest-building.

	Number of visits to the nest			Percentage frequency of visits to the nest		
	Female	Male	Total	Female	Male	Total
P1R	375	156	531	71	29	100
P2R	83	1	84	99	1	100
P1B	71	38	114	73	27	100
P2B	51	12	63	81	19	100

Nest-building by the male decreased as the nest neared completion (Table 10). At the beginning of the construction of Nest 1 there was a

FIGURE 4. Diurnal variation in the number of visits to the nest.



significant difference in the number of visits to the nest by the male and female ($\chi^2 = 8.6$, df = 1, p = 0.05), but as the nest neared completion there was an even greater significant difference in the number of visits by the male and female of P1R ($\chi^2 = 63$, df = 1, $p > 0.001$). Af the later stages of nest construction he spent more time foraging, "Courtship feeding" and displaying. There also appeared to be an even greater decrease in building by the male once the first clutch fledged. At this stage his time was spent feeding the young while the female built. I did not obtain quantitative information on this aspect because more time was spent collecting data on fledgling behaviour than on nest-building. However, the young were fed in the nest-site, and the sex of the bird building nearby was noted frequently.

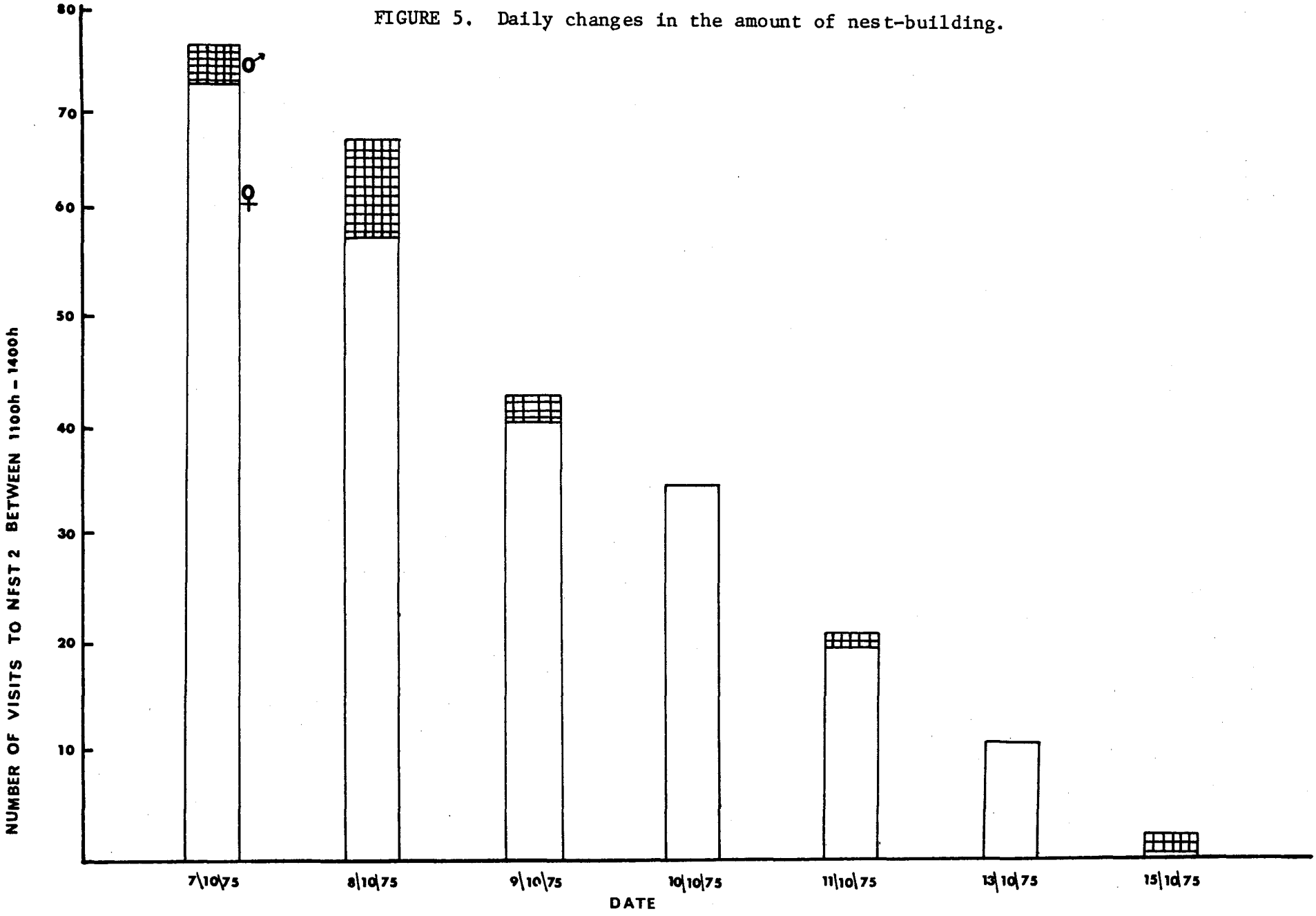
TABLE 10. Changes in P1R male's participation in nest building as the nest was built.

Nest	Stage of construction	Total number of visits by both sexes	Visits by the male only	Percentage of visits by the male
1	beginning	67	25	37
	end	53	6	11
2	beginning	83	6	7
	end	11	0	0
3	beginning	112	29	26
	end	62	2	3

There appeared to be some diurnal variation in the intensity of nest-building, most of which occurred between 0600h and 1100h. There was a drop in the number of visits during the afternoon and a large decrease after 1500h (Fig. 4). This decrease may be due to the need to feed before the night rest period.

There also appeared to be a daily change in the amount of nest-building, i.e., as building progressed, the number of visits to the nest

FIGURE 5. Daily changes in the amount of nest-building.



decreased from day-to-day (Fig. 5). This trend was apparent when nest-building was spread over a number of days but may not occur in nests built over one or two days.

5.3.4 Nest-building Techniques

Nest construction involves the integration of a number of stereotyped movements, which in this bird as in others are probably characteristic of the species (Thomson 1964). Four apparently stereotyped movements were identified in the South Island Fantail.

(i) "Head-rim" movements. With its bill the bird grasped nest material projecting from the outer surface, then pulled and pushed the nest material into the rim of the nest. The bill was then pulled across the rim to shape it.

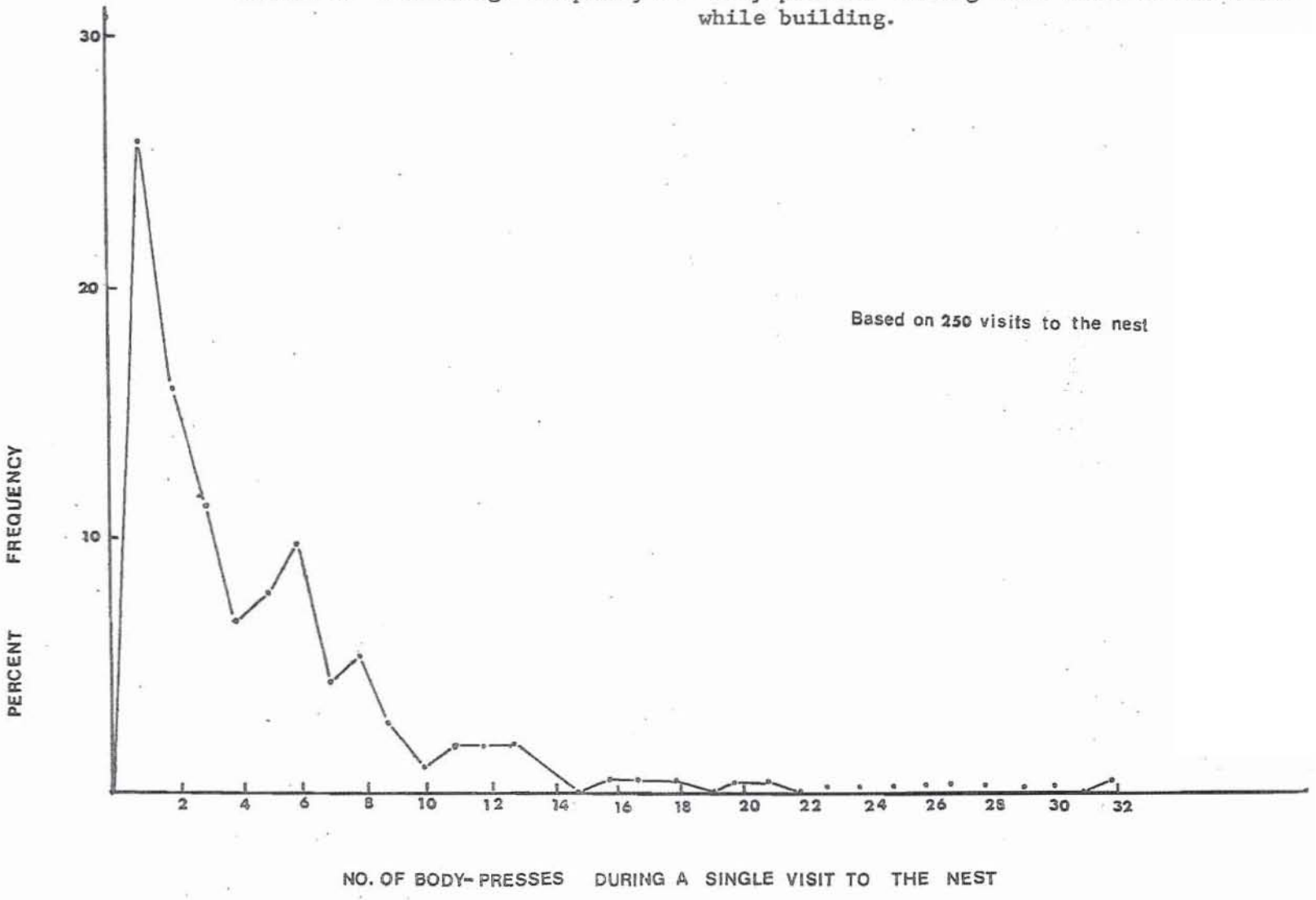
(ii) Turning. While crouched the bird rotated in the nest. The bird's tail was held approximately 45° above the level of the back as the bird turned both clockwise and anticlockwise in the nest-bowl. The fantail did not always make a complete revolution but often stopped and turned in the opposite direction.

(iii) "Wiping". The bill was wiped (1.5 centimetres below the outer surface of the rim) halfway around the nest. This shaped the outer surface and was a means of transferring cobwebs from the bill to the nest. The wings fanned to help maintain balance.

(iv) "Body-presses". In this movement the bird lowered its body into the nest and appeared to press downwards. At the same time the closed tail was pressed against the nest-rim and quivered rapidly from side-to-side. In between each "Body-press" the bird stood up in the nest and raised the tail such that it was positioned at right angles to the body surface.

In a less common movement the birds clung to the outside of the nest, pulling and pushing loose strands into place.

FIGURE 6. Percentage frequency of "Body-presses" during each visit to the nest while building.



On landing the bird performed "Head-rim" or "Wiping" movements rather than "Body-presses" (χ^2 = 137, df = 1, p > 0.001) which were frequently given before leaving (Table 11).

TABLE 11. Building movements used on entering and leaving the nest.

	On entering		On leaving	
Building movement	Number of observations	Percentage frequency of observations	Number of observations	Percentage frequency of observations
"Head-rim"	58	54	25	23
"Wiping"	39	36	10	9
"Body-press"	11	10	73	68
Total	108	100	108	100

"Body pressing" occurred later in the building sequence. As many as 32 presses in a single visit were noted but one, two and three presses were more common (Fig. 6).

5.3.5 Nest Desertion

Fifty-nine per cent of the 14 Christchurch nests (Table 1) were deserted prematurely, three before egg-laying, two during incubation, and three while brooding.

5.3.6 Re-use of Nests

I observed the re-use of a nest once in this study. A pair (P2B) which had raised two clutches successfully rebuilt their second nest and laid a third clutch there at the end of the breeding season (Table 1).

5.4 DISCUSSION

The selection of a nest site and construction of a nest are the first major tasks of a pair of birds in the breeding season.

The South Island Fantail selected nest sites two to eight metres above the ground. The range was not as great as that exhibited by the Willie Wagtail. Marchant (1974) found that the Willie Wagtail nested from below one metre to higher than 15 metres. The difference in these results is probably due to differences in the number of nests analysed (i.e., this study is based on 19 nests, whereas Marchant's analysed 565 nest-records). In some species of passerines the same bird may build its nest at different heights above the ground according to the season (Nice 1937, Walkinshaw 1959). This phenomenon was not apparent in the fantail, the difference being attributed to differences in the habitat of the fantail and those species in which seasonal variation in height of nests above the ground exists. In the Field Sparrow *Spizella pusilla* (Walkinshaw 1959) and the Song Sparrow *Melospiza melodia* (Nice 1937) the seasonal rise in nest altitude paralleled, and probably was stimulated by, the rising growth of grasses and other vegetation. The vegetation of the fantail's habitat remained unchanged during the breeding season. Preston and Norris (1947) noted that within a given species, some individuals persistently nest high and others low and that an individual does not vary its nesting height over the whole range used by the species. However, this was not the case in the South Island Fantail. The four pairs of fantails in Christchurch showed variations in the height of successive nest sites during one breeding season (Table 7). As long as the nests are concealed and well protected there is probably no great advantage in birds showing a preference for a particular height at which to nest. The fact that the fantail nested on exotic trees clearly shows that this species has become well adapted

to changes introduced by man. A similar conclusion, with respect to the Willie Wagtail, was made by Marchant (1974).

Birds use their nests chiefly to protect themselves, their eggs, and particularly their developing young from predatory animals and from adverse weather conditions during the breeding season, the most vulnerable period in the life cycle (Welty 1962). These functions are accomplished in the fantail by nesting at the tips of tree branches, in areas of dense foliage and by using nest material found in the immediate vicinity, thus assisting in camoflaging the nest.

The nest-site appeared to be selected by both the female and male. However, because very few observations on nest site selection were made, further research on this aspect may prove this to be atypical for the species. In many birds there is often an appreciable interval between nest site selection and the start of nest-building. The interval may range from several weeks or months down to a day (or less) depending on the bird's drive to breed, weather conditions, and clutch number (Thomson 1964). The selection of the site for Nest 1 began in a warm spell at the end of winter, and building started seven days later (Table 1, Fig. 3). This differed from the two day interval between the desertion of Nest 1 and start of Nest 2. A similar decrease in the interval between nest site selection and building as the season progressed was recorded for all fantails studied (n = 4). This trend is probably attributed to an increasing need to nest and lay before weather conditions deteriorate and food availability decreases as the breeding season ends.

Nest materials used vary widely from one species of passerine to another. Nest material used by the South Island Fantail (Section 5.3.3) was similar to that used by the North Island Fantail (Oliver 1930, Coates 1960, Blackburn 1965, Brockie 1971) and overseas birds - the

Willie Wagtail (Brown 1949, Marchant 1974), the Northern Fantail *Rhipidura rufiventris* (Frith 1976) and the Burmese White Browed Fantail Flycatchers *R. aureola burmanica* (Deignan 1945). All these species face the outside of their nests with cobwebs. Unlike the South Island Fantail, which collects cobwebs by pecking at the webs and wiping the bill against the nest, the Willie Wagtail flies through the web and pecks the cobweb off the body (Brown 1949) before wiping it against the nest. It is difficult to determine which method of cobweb collection is more effective. Although the Willie Wagtail probably collects more web faster, to bind the nest, the bird's flying efficiency is probably reduced until the cobwebs are removed from the flight feathers and so the danger of predation is probably greater than if the bird had merely collected the web in the bill.

In many species the female builds the nest alone. In others the female builds the nest with the assistance of the male. Oliver (1930) and Stead (1932) noted that both the female and male fantails share the work of building, but my results show a greater participation by the female (Table 9). Not only did she make more visits to the nest but she also spent longer periods building. In some species, although the male makes fewer trips to the nest, he brings bigger loads. This was not apparent in the fantail; indeed, the male often entered the nest without nest material. The reason for the differences in participation of the sexes in nest-building is difficult to determine because the male does follow the female to the nest and does not substitute nest-building for the defense of territorial boundaries. However, the experience of building most of the nest by the female may result in a very strong attachment to the nest and site by her. Differences in the role of the male in nest-building in this study, and Oliver's (1930), may be due to the fact that Oliver's conclusions were based on very few observations.

Although the female did most of the building, nest-building by the male decreased further as the nest neared completion (Table 10). This was due to the fact that he spent more time foraging, "Courtship feeding" and displaying at this stage. There appeared to be an even greater decrease in building by the male once the first clutch fledged. At this stage his time was spent feeding the young while the female built. I did not obtain quantitative information on this aspect because more time was spent collecting data on fledging behaviour than on nest-building. However, the young were fed in the nest-site and the sex of the bird building nearby was clearly noted. Marchant (1974) also noted that only one adult builds if young from an earlier nest are still dependent.

The time consumed in building a nest depends on a number of variable factors such as the size of the nest and its complexity; the materials used and the distance they are carried; the species building the nest; whether one or both members of the pair do the building; the age and experience of the builder; the time of year and weather; and the geographic latitude (Welty 1962). As a rule, small passerines build their nests in a few days. In the South Island Fantail, first nests took 11 to 26 days to build but third and fourth nests were built in two or three days. The decrease in the time taken to build later nests probably results from a need to build before weather conditions deteriorate near the end of the breeding season, and to the experience gained in building earlier nests.

The principal movements in nest-building in the South Island Fantail are similar to those employed by other passerines (Thomson 1964, Pettingill 1970). These movements are innate, derived and then stereotyped from such sources as maintenance activities or even irrelevant behaviour. Similar "Head-rim", "Wiping" and "Turning movements" have

been reported in other passerines, however, no information other than a description of these movements could be found. In this study I found a tendency to perform "Head-rim", or "Wiping" movements on entering the nest and a tendency to "Press" into the bowl before leaving. This tendency is probably due to an apparent need to place material held in the beak on entering the nest, rather than shape. Differences in the amount of "Body-pressing" during a single visit to the nest is probably an instinctive response and subject to individual variation.

A number of factors causing nest desertion in some species of *Rhipidura* have been recorded and include: adverse weather conditions before egg-laying (Blackburn 1966); interference of the nest by larger, more aggressive birds (Lord 1953), and disturbance of the nest by predators, or man, before the young hatch (Frith 1976). Although disturbance by an observer cannot be entirely ruled out, I agree with Cunningham (1954) who wrote "I have not known a fantail's nest to be deserted through being watched". I took great care when near the nest and the birds did not appear to be disturbed, i.e., they did not approach or give aggressive calls.

Fifty-nine per cent of the 14 Christchurch nests were deserted prematurely, three before egg-laying, two during incubation, and three while brooding.

Desertion was attributed to four main factors:-

(i) weather conditions. Building of the first nests began in a warm late-winter spell and was spread over a long period, during which time the weather became colder and probably unsuitable for egg-laying,

(ii) disturbance by the Riccarton Bush Ranger. The Ranger continually cleared and burnt the bush near the nests. While I was absent he mowed within 60 centimetres and burnt a fire two metres from an incubating pair. They deserted the next day,

(iii) nest desertion by a neighbouring pair. If neighbours nested in close proximity the male's nest attentiveness appeared to be synchronised; i.e. , both males were attentive at the same time. If one pair deserted their nest, the male spent most of his time singing at the territorial boundaries. The incubating male (of the neighbouring pair) then left the nest to fight or engage in song bouts, disturbing his and his mate's incubation rhythm (Section 6.3.5). The eggs were often left unattended. The female spent more time incubating and less time feeding. This was followed by desertion in the case of Nest 3, and

(iv) predation. One nest was deserted after its three 7-day old nestlings disappeared. Brown rats and feral cats are present in Riccarton Bush and are likely to be predators of nestling fantails.

The fantail builds a nest for each clutch and "the second use of a nest is quite exceptional" (Blackburn 1966). However, the re-use of nests has been noted in the Northern Fantail (Lord 1953) and the North Island Fantail (Coates 1966, Flux 1974). Re-use of a nest was noted in this study. Although building a new nest for each generation of young is expensive in labour, it minimizes the chances of disintegration of a nest while it is sheltering eggs or young and reduces the possibility of the accumulation of nest parasites (Welty 1962). As the breeding season ends, and if the pair has already raised one or two clutches successfully, old nests are probably re-occupied to save energy and time before weather conditions deteriorate as the breeding season ends.

CHAPTER 6

CHAPTER 6

INCUBATION BEHAVIOUR

6.1 INTRODUCTION

Incubation behaviour comprises the special movements and organisation of daily activity shown by birds when they have eggs (Thomson 1964).

With the exception of a study on the breeding activities of the Willie Wagtail (Roberts 1942) little is known about the incubation period of the Willie Wagtail, observations on the behaviour of incubating parents were not made.

In this chapter incubation behaviour is discussed under the headings: incubation period, nest attentiveness, variations in attentiveness, length of time the nest is left unoccupied during nest-relief, and nest-relieving behaviour.

6.2 METHODS

The incubation behaviour of three pairs at seven nests was studied. Observations of five pairs at Kowhai Bush, Kaikoura, supplemented these results.

Standard observations made during two to four hour observation periods included:-

(i) the sex of the bird arriving at the nest. Birds were identified by paint markings previously placed on the underside of the tail, or by individual differences in plumage,

(ii) the sitting position of the bird in the nest,

(iii) the behaviour of the fantail off the nest, i.e., number of songs given, length of song, feeding behaviour and territorial defence,

(iv) the behaviour of the birds during nest-relief,

(v) the time the bird spent on the nest, i.e., "nest attentiveness" (Pitelka 1941);

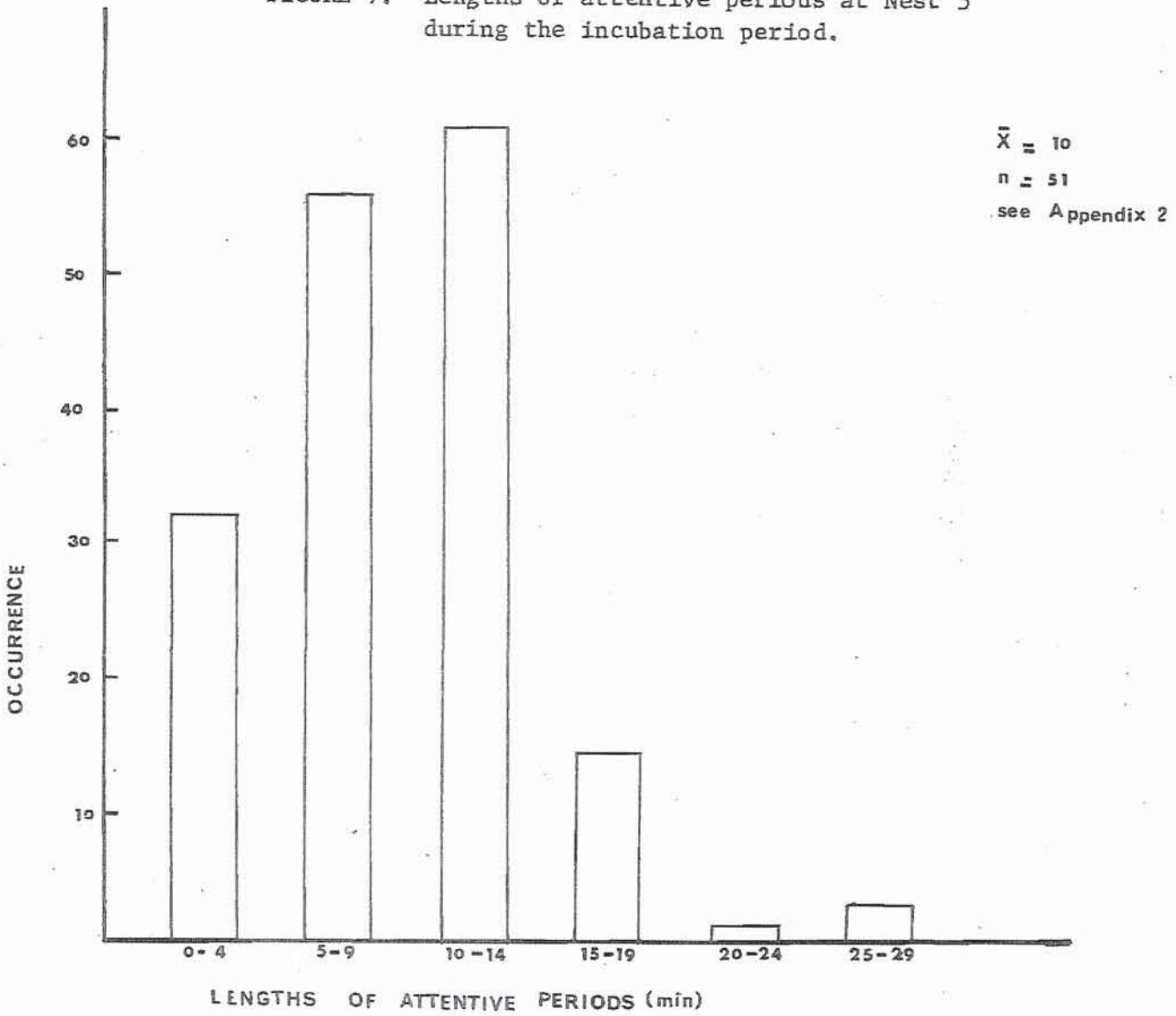
(vi) the time the nest was left unoccupied during nest-relief, and

(vii) a check of the sexes was made by quietly approaching the nest and noting the paint markings. The presence or absence of song during attentive periods also aided as a check on the sex of the bird concerned (Section 10.3.3b).

Attentive periods were recorded for both sexes. A detailed study of six nests by three pairs was made and less detailed results from another seven nests were noted. Recordings were made during two to four periods between 0600h and 2000h throughout the incubation period, and those taken between 0900h and 1700h at one nest were lumped to obtain information on differences between sexes, pairs and successive clutches. Although detailed results on diurnal variation in attentiveness were not obtained, nest attentiveness appeared to remain constant throughout the day (Fig. 4). Consequently, there was no need to obtain information on incubation behaviour at exactly the same time each day. Nevertheless early morning and late evening observations have not been included in case variations in incubation behaviour during these periods existed.

The presentation of incubation data follows that prescribed by Pitelka (1941). This requires information on the range of nest attentiveness rather than variance or standard deviation. Some standard deviations were calculated but because of the effect of a few high and low readings they did not provide a true index of the situation. For instance, although the length of attentive periods at Nest 5 clumped about the mean (10 minutes) the variance (10·0) standard

FIGURE 7. Lengths of attentive periods at Nest 5 during the incubation period.



deviation (3·1) does not convey this information (Fig. 7).

Because of the height of most nests (Section 5.3.1), egg-laying dates and information on the behaviour of birds in the nest are unknown.

6.3 RESULTS

6.3.1 Incubation Period

In this study the incubation period refers to the time between the start of a regular, uninterrupted incubation and the emergence of the young (Pettingill 1970). The incubation period was thus estimated to extend from the third day to the first in which pivoting and "Feeding vocalisations" were observed at the nest (Section 7.3.1).

Thirteen day incubation periods were recorded at two nests, and 14 days at another two (Table 12). Nice (1936) suggested that variations such as this could be due to occasional postponement of the start of incubation, interruptions due to irregular attendance by the parent, and inclement weather.

TABLE 12. Incubation periods.

Nest	Incubation period (days)
5	14
6	14
7	13
13	13

Because of the small sample (i.e., four nests) and lack of information on laying dates, these results are perhaps not representative of the species.

FIGURE 8. Length of time Nest 6 was left unoccupied during nest relief.

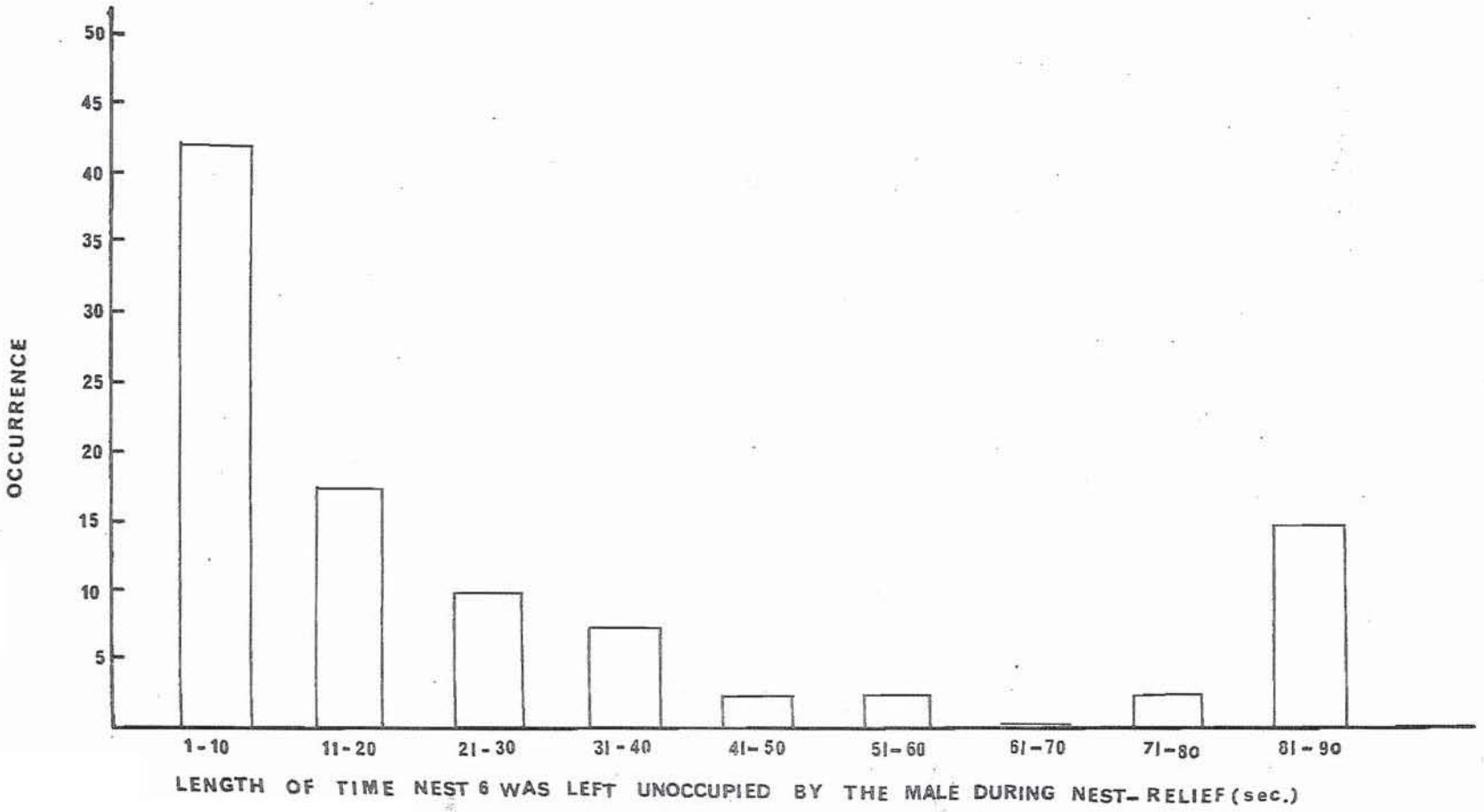
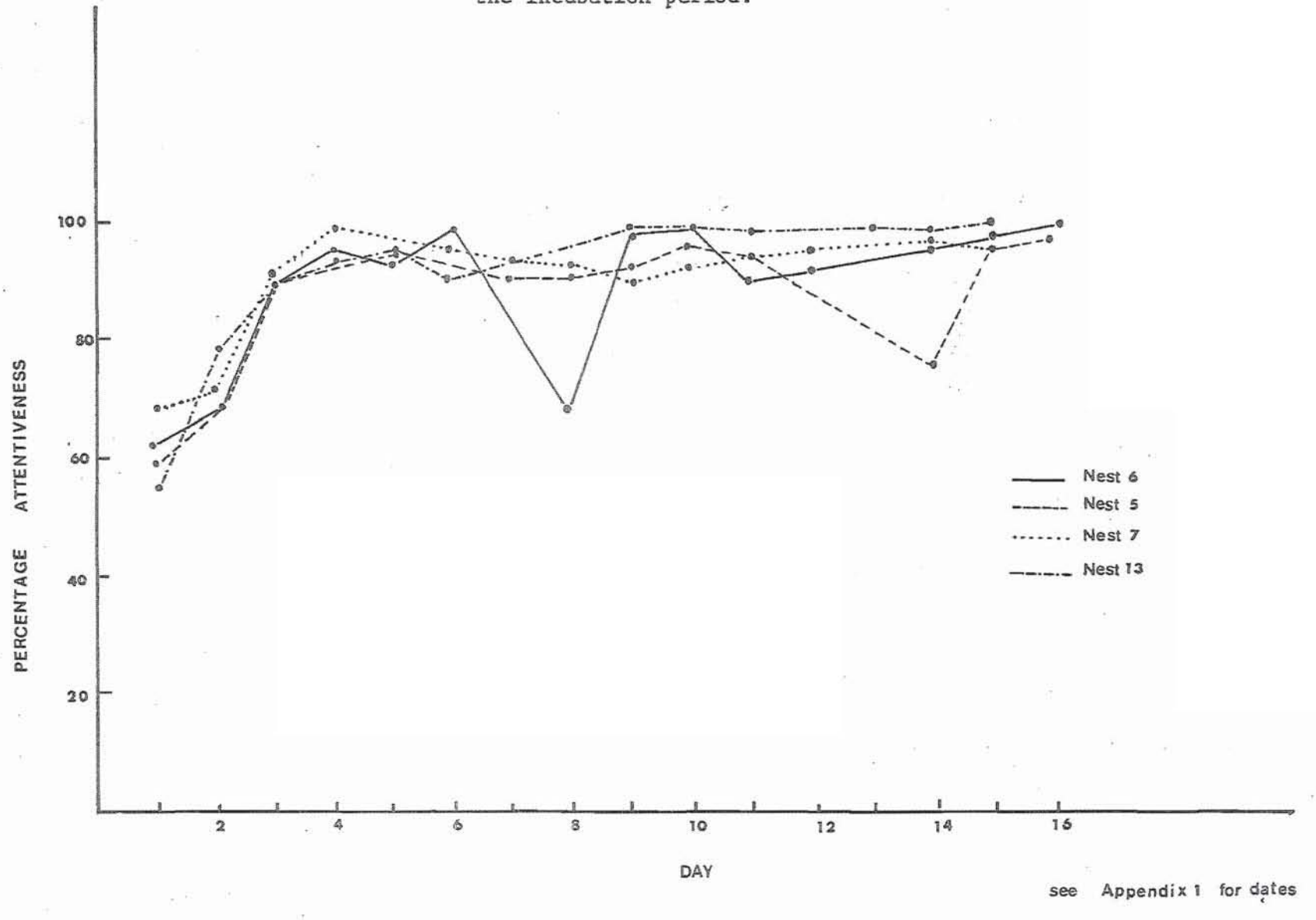


FIGURE 9. Percentage attentiveness throughout the incubation period.



6.3.2 Nest Attentiveness (0900-1700h)

Both sexes incubate. The length of the female's attentive period ranged from 0.5 to 58 minutes, with a mean of eight and 14 minutes at the first and second nests respectively (Table 13).

There were no significant differences ($t = 1.53$, $df = 103$, $p = 0.1$, Appendix 1) in the mean period of attentive spells by the P2R male and female (Table 13). However, there was a significant difference ($t = 4.5$, $df = 93$, $p = 0.01$, Appendix 2) in the length of attentive spells at P2R first and second nests.

Although the length of attentive periods ranged widely, they clustered about the mean (Fig. 7). The extreme values were due to infrequent circumstances, e.g., hail storms and attacks on neighbouring fantails.

In the first two days of incubation the nest was often left unoccupied for long periods. Consequently nest attentiveness was low until the third day when incubation proper, with a high nest attentiveness (Fig. 9), began.

Both parents made an average of three visits per hour to their first nest and two visits per hour to their second (Table 14). Because the time the nest was left unoccupied remained relatively constant, the decrease in visits was a result of longer attentive periods at each visit.

6.3.3 Length of Time the Nest was left Unoccupied during Nest-Relief

The length of the periods in which the nest was left unoccupied ranged widely (Table 15) and did not cluster about the mean (Fig. 8). Recordings at one end of the range (i.e., 0.5 secs) were due to a bird remaining until its mate landed on the nest, and at the other end (630 secs) to:-

TABLE 13. The length of attentive spells (min.) by the female and male at first, second and third nests.

Nest *	P2B		P1R		P2R		Average	
	Female	Male	Female	Male	Female	Male	Female	Male
First	—	—	$\bar{X}$ = 6 R = 1.5–13 n = 21	$\bar{X}$ = 8 R = 0.5–17.5 n = 24	$\bar{X}$ = 10.5 R = 2.5–26.5 n = 51	$\bar{X}$ = 9 R = 1–14 n = 54	$\bar{X}$ = 8 R = 1.5–26.5 n = 72	$\bar{X}$ = 8.5 R = 0.5–17.5 n = 78
Second	$\bar{X}$ = 14.5 R = 7–22.5 n = 17	$\bar{X}$ = 18.5 R = 12–31 n = 13	$\bar{X}$ = 11 R = 0.5–31 n = 30	$\bar{X}$ = 10 R = 0.5–41 n = 29	$\bar{X}$ = 16 R = 0.5–58 n = 44	$\bar{X}$ = 15 R = 2–32 n = 39	$\bar{X}$ = 14 R = 0·5–58 n = 91	$\bar{X}$ = 14.5 R = 0·5–41 n = 81
Third	—	—			$\bar{X}$ = 18 R = 6.5–39 n = 14	$\bar{X}$ = 14 R = 2–25 n = 18	$\bar{X}$ = 18 R = 6·5–39 n = 14	$\bar{X}$ = 14 R = 2–25 n = 18

$\bar{X}$ = mean length of attentive spell, R = range of attentive spells, n = number of attentive spells.

* First, second and third nests for each pair refer to those in which eggs were laid. They do not refer to nests deserted before egg-laying.

TABLE 14. Number of visits/h to first and second nests.

Nest	P2B		P1R		P2R	
	Female	Male	Female	Male	Female	Male
First nest	—	—	$\bar{X} = 3$ R = 0–6 n = 12	$\bar{X} = 3$ R = 1–6 n = 12	$\bar{X} = 3$ R = 2–6 n = 17	$\bar{X} = 3$ R = 2–7 n = 17
Second nest	$\bar{X} = 2$ R = 0–5 n = 14	$\bar{X} = 1.5$ R = 0–4 n = 14	—	—	$\bar{X} = 2$ R = 1–5 n = 21	$\bar{X} = 2$ R = 1–5 n = 21

$\bar{X}$ = mean number of visits/h, R = range of the number of visits/h, n = number of one hour observation periods.

TABLE 15. The length of periods the nests were left unoccupied.

Pair	Nest	Length of period the nest was left unoccupied (sec)	
		Female	Male
P1R	2	$\bar{X}$ = ? R = 0.5 - 7.0 n = 12	$\bar{X}$ = 5.5 R = 0.5 - 34 n = 15
P1R	3	$\bar{X}$ = 40 R = 0.5 - 551 n = 29	$\bar{X}$ = 47 R = 0.5 - 314 n = 29
P2R	5	$\bar{X}$ = 40 R = 0.5 - 35 n = 52	$\bar{X}$ = 90 R = 0.5 - 561 n = 561
P2R	6	$\bar{X}$ = 12.5 R = 1-89 n = 43	$\bar{X}$ = 61 R = 0.5 - 630 n = 40
P2R	7	$\bar{X}$ = 36 R = 1-327 n = 16	$\bar{X}$ = 166 R = 1-630 n = 21
P2B	2	$\bar{X}$ = 15 R = 1-147 n = 14	$\bar{X}$ = 63 R = 1-273 n = 8

$\bar{X}$ = mean period of time the nest was left unoccupied, R = range in the length of periods the nest was left unoccupied, n = number of times the nest was left unoccupied.

(i) the failure of a bird to return and relieve its mate.
If a bird's attentive period was unusually long, because the mate failed to return, the bird often flew off the nest and it was left unoccupied for quite long periods (630 secs), and

(ii) desertion of the nest shortly after relieving a mate.
In many cases the cause was unknown. Occasionally the bird left to chase an intruding fantail.

There was a significant difference ($t = 2.2$, $df = 98$, $p = 0.01$, Appendix 4) in the time the P2R male and female left Nest 6 unoccupied. There was a tendency among females to stay on the nest until their mates were close by, whereas the male often left before the female returned to the nest-site. This indicates a stronger motivation in the female to remain on the nest.

6.3.4 Variations in Length of Attentive Periods as Incubation Progressed from Day to Day

Although there was no change in the total time the nest was occupied as incubation progressed from day to day (Fig. 9), there was a change ($t = 1.02$, $df = 18$, $p = 0.3$, Appendix 5) in the length of each attentive period from day to day (Table 16). In P2R there appeared to be a general increase in the length of the periods from the start of incubation of the first clutch (12 September 1975) to the end of incubation of the second clutch (30 October 1975). By 17 November 1975 the length of the attentive periods had decreased but were still longer than those recorded at the first nest (Nest 5). Similar trends were noted at other nests.

TABLE 16. Increase in the length of attentive spells as incubation progressed from day to day.

Nest	Date	Mean length of attentive spells (mm)	Range of attentive spells (min)	Number of attentive spells
5	12/9/75	9	8 - 20.5	23
	13/9/75	9	3 - 17.0	15
	16/9/75	9	2 - 16.0	10
	18/9/75	11.5	1 - 725	11
	19/9/75	12.5	8 - 18	9
	20/9/75	10	2 - 19	10
	24/9/75	8	2 - 13	14
6	20/10/75	15	12 - 20	12
	22/10/75	19	11 - 27	8
	24/10/75	20	17 - 22	10
	26/10/75	16	2 - 25	8
	28/10/75	16	7 - 26	11
	30/10/75	20	10 - 25	9
7	17/11/75	16	9 - 20	8
	19/11/75	14	3 - 25	12
	25/11/75	13	2 - 25	11

* Results for Pair 2 Riccarton Bush.
Difference between 20/ 9 /75 - 24/10/75, $t = 1.02$, $df = 18$, $p = 0.3$.

6.3.5 Variations due to Desertion of Neighbouring Nests

Before P2R deserted Nest 6, the male and female of their neighbouring pair (P1R) spent relatively equal periods on the nest. However, there was a decrease in incubation by P1R male and an increase in the time the nest was left unoccupied the day after P2R deserted (Table 17).

Before P2R deserted, the female of P1R stayed on the nest until her mate was nearby, and returned as soon as the male left. This behaviour resulted in a generally high nest attentiveness. The female rarely left the nest unoccupied. Although the male left the nest unoccupied for short periods, he left it for slightly longer periods than the female. After P2R deserted, P1R male stayed on the nest for much shorter periods, deserting it many times to fight or engage in

singing bouts with the P2R male, and the amount of attentiveness by the male decreased (Table 17).

TABLE 17. Change in attentiveness by P1R after the desertion of Nest 6 by P2R.

Date	Length of observation period (min)	Percentage attentiveness	
		Female	Male
5/11/75	183	53	44
7/11/75	178	59	35
9/11/75	137	59	29

6.3.6 Nest-Relief

"Type 1" calls were given four to six metres from the nest as the male or female approached to relieve its mate. Other activities, viz. Song, "Type 2" vocalisations, feeding and preening, occurred less frequently (Table 18).

TABLE 18. Behaviour of the fantail as it approached the nest.

Behaviour	Number of observations	Percentage frequency of observations
Stopped before entering and gave "Type 1" calls	234	72
Performed the Nest-relief display	36	12
Stopped and sang	28	7
Made a direct flight	16	5
Stopped and gave "Type 2" vocalisation	6	2
Hawked	3	1
Stopped and preened	2	1
Total	325	100

Occasionally the bird made a direct flight to the nest (Table 18) but usually perched on a nearby tree for several seconds before flying

in.

In 34% of 61 observations the attentive bird waited for its mate to land on the nest (Table 19). This behaviour was more apparent in the female. In most cases (54%) the attentive bird flew out as the other called from a nearby perch or flew towards the nest.

TABLE 19. The behaviour of the attentive fantail during nest-relief.

Behaviour	Number of observations			Percentage frequency of observations
	Female	Male	Total	
Left before the other reached the nest	16	17	33	54
Left when the other landed on the nest	14	7	21	34
Left before the other was in the nest-site	2	5	7	12
Total	32	29	61	100

Occasionally one of the fantails (usually the male - see Table 19) flew out before its mate returned to the nest. When the male left, the female quickly responded to his songs near the nest and returned so that the time the nest was left unoccupied was very short. However, when the female left (before the male returned) she flew away from the nest without calling or singing and, presumably because her desertion was not conveyed to the male, the period the nest was left unoccupied was greater than when the male left. If the male returned to find her feeding or resting (instead of on the nest) he usually chased and gave "Type 2" vocalisations around her.

The male rarely left the nest-site before the female entered the nest. On leaving the nest he continuously sang or gave "Type 2" vocalisations until she returned. As soon as she appeared he flew

towards her, then followed her to the nest. As she entered the singing stopped abruptly and the male flew away.

If a bird returned shortly after being relieved, its mate gave soft "Contact type 1" calls from the nest. This appeared to encourage the approaching bird to turn and move away again.

The birds tended to sit in the same position on each visit to the nest (Table 20). This was usually the point at which each bird landed on the nest, and because flight paths into the nest remained fairly constant, the sitting positions did too.

TABLE 20. Frequency of sitting positions.

Pair	Nest	Total number of observations	Percentage frequency of observations at each position on the nest *							
			1	2	3	4	5	6	7	8
P2R	5	57	2	61	7	0	9	23	0	0
P2R	6	70	0	0	1	5	2	15	25	22
P1R	2	23	4	4	0	4	0	22	39	26
P1B	3	35	8	60	0	9.5	9.5	9.5	0	6
P2B	12	23	4	9	35	30	17	4	0	0
P2B	13	37	0	0	1	0	2	19	12	3

* The sitting positions were relative to the observer and are not related to compass readings. Therefore, one nest cannot be compared with another.

After landing, the birds "Settled" on the eggs. "Settling involves "ruffling" or lowering of the abdominal feathers to expose the brood-patches and a waggling or quivering action as, or after, the bird lowers itself" (Thomson 1964).

The tail was held in one of three positions during incubation:-

(i) just above the horizontal position. This was noted when the bird was awake and fairly active on the nest, i.e., when there was quite a lot of head movement,

(ii) below the horizontal position, or

(iii) vertically up with respect to the body. This position was frequently observed in windy conditions and twice in hail storms.

In most cases the bird sat quietly on the nest but occasionally lifted, placed its bill into the bowl, resettled and performed the "Head-forward" movement (Section 8.3.2e). It also preened, scratched and stretched its wings occasionally.

A large amount of restlessness was noted at the beginning and end of an attentive spell. The fantail constantly peered around and over the nest, watching any movement outside.

When the mate returned, the attentive bird tended to fly out in the direction opposite to the one coming in (Table 21), which was usually in the direction it faced in the nest. Occasionally the bird lifted, turned and flew towards the other.

TABLE 21. Direction of flight out of the nest.

Behaviour	Number of observations	Percentage frequency of observations
Cases in which the bird left the nest in the direction opposite to the one flying in.	109	68
Cases in which the bird flew out towards the approaching one.	51	32
Total	160	100

After leaving, the bird landed on a nearby perch and usually preened, stretched, gave "Type 2" vocalisations or "Bill-wiped" (Table 22). The male always sang before flying out of the nest-site.

TABLE 22. Behaviour given immediately after leaving the nest during incubation.

Behaviour after leaving the nest	Number of observations	Percentage frequency of observations
"Type 3" vocalisation	74	32
Preened	40	18
Stretched	33	15
"Type 2" vocalisation	5	2
"Bill-wiped"	14	6
Flew straight out of Nest-site	3	1
"Type 1" calls	26	11
"Hawked" or "Aerial fed"	11	5
Scratched	10	4
Pecked at foot	1	1
Chased another fantail	11	5
Total	228	100

6.4 DISCUSSION

"Incubation - the process by which the bird applies its body heat to the eggs" (Pettingill 1970) and the accompanying behaviour have been given more attention than many other phases of the breeding cycle, but the subject is far from exhausted; information is still lacking for a wide variety of species. One such species is the New Zealand Fantail, for which little information is available other than an estimation of the incubation period (Blackburn 1965, Soper 1972). A large amount of research has been centred around the study of incubation periods in passerines and there has been much discussion on the definition of

incubation period. "In some cases it has been considered as the time the parent sits on the eggs. In some it is reckoned from the laying of the first egg of the set until its hatching, in others from the laying of the last egg to hatching of the first, and in still others no explanation is offered as to what is meant" (Nice 1954). Fautin (1941) considers that the start of incubation in passerines varies from the time the first egg until the third egg was laid, but in most cases begins with the deposition of the second egg. I could not use any of these definitions as a means of estimating the incubation period of the fantail because most of the nests were too high to establish egg-laying dates. Instead the estimation of the incubation period was based on a behavioural criteria noted by Ryves (1943). He found that "steady incubation" was characterised by regularity in attentive and inattentive periods. In many species, steady incubations begin after an initial period of "casual brooding" which is usually irregular and haphazard. "It is only when such brooding gives place to incubation proper that development of the eggs commence" (Ryves 1943).

By noting attentiveness once nest-building had finished it was possible to determine the point at which incubation began. In a study of five nests the percentage attentiveness, during a standard period between 0900h and 1700h, increased from an average of 60% on Day 1 to 89% on Day 3 (Table 13). From Day 3 the attentiveness remained fairly constant (Fig. 9). Because of the change in attentiveness and regularity in attentive spells, Day 3 was taken as the start of incubation, which lasted 13-14 days. Differences in the incubation period between the South Island Fantail, the North Island Fantail, whose incubation period has been estimated as 15 days (Blackburn 1965, 1967), and the Willie Wagtail, who has an incubation period of approximately 14 days (Marchant 1974), may be due to variations in the

methods of estimating the incubation period. I emphasise the need to note the laying data as well as the percentage attentiveness over the first few days of egg-laying, when, presumably because of the gradual physiological changes that result in broodiness behaviour, birds spend short periods on the nest. Regular incubation does not always begin at the laying of the first or last egg and, unless thermocouples are available to obtain temperature readings in the nest, the method I used appears to be more useful than the common definitions of incubation period based on egg-laying dates.

Although some reference has been made to the fact that the female and male fantail take part in incubation, no prior information is available on the amount of incubation done by each parent. In this study I found that the female and male share incubation equally. Skutch (1957) suggested that equal sharing of incubation is probably a primitive method. Welty (1962) noted that variation in the role of the sexes in incubation may depend on habitat or type of nest. For instance, one-parent incubators are common among birds which nest in the open because the fewer birds there are around the nest the less conspicuous it is to predators. This does not apply to those which nest in holes, where protection against predators is more assured. I believe that because conspicuousness about the nest does not result in a marked decrease in hatching success and reproductive efficiency in the fantail, the primitive and less common method of incubation being shared equally by both sexes has persisted in this species.

For some species in which both sexes incubate, the eggs may be covered almost constantly during the incubation period, but in the majority of species the eggs are incubated only part of the time each day (Van Tyne and Berger 1966). Attentiveness is the term used to refer to the time the bird spends on the nest; inattentiveness, the time the

bird is off the nest. In most passerines the per cent attentiveness ranges from 78% to 90% (Van Tyne and Berger 1966). The fantail shows a very high nest attentiveness of 90% to 98% (Fig. 9). This was probably due to the fact that both parents showed a high motivation to incubate, rarely leaving the nest before the mate returned. At the first nest the female and male spent an average of 8.5 minutes on and off the nest. However, I found that there was a significant increase in the length of attentive spells at the second nest (Table 13). The increase from 8.5 to 14.5 minutes could be due to experience by the fantails, or changes in the availability of food. Because the length of attentive spells appears to be determined by the length of inattentive periods (i.e., a bird usually waited on the nest until its mate returned), the increase in the length of attentive and inattentive spells could be due to a decrease in abundance of food. With less food available more time is required to catch prey before returning to relieve the mate. Very little work appears to have been concentrated on changes in length of attentive periods with successive clutches. This study indicates that such changes do occur, however, a more detailed study on this aspect in the fantail and other passerines is warranted.

Another aspect of incubation behaviour which has attracted little attention includes differences in the time the female and male leave the nest unoccupied during nest-relief. In this study the significant difference in the time the female and male fantail left the nest unoccupied indicates a higher motivation in the female to remain on the nest.

The behaviour of the male fantail during incubation resembles the general behaviour of most passerine species. He spent his time off the nest moving over the territory, vigorously singing at song posts throughout his territory, feeding and resting. The male fantail came to

the nest more or less regularly to relieve the female. He signalled his presence by giving a large number of "Type 1" calls as he approached the nest. The behaviour of the attentive fantail, regardless of the sex, also resembled that of other passerine species. Behaviour on the nest involved "Settling", which probably served to bring the brood-patches into the closest contact with the surfaces of the eggs (Beer 1961), moments of restlessness, during which it changed sitting positions, and a movement called "shifting" in which the standing bird bends its head down and moves the eggs about by rolling them with the underside of its bill (Thomson 1964).

In most passerines the departure and return of the parents from and to the nest are deliberate and secretive (Pettingill 1940). This is not the case in the South Island Fantail. Both sexes give a large number of loud "Type 1" calls as they approached to relieve their mate. An "Aerial nest-relieving" display which involved a large amount of aerial acrobatics close to the nest, making the bird conspicuous to its mate, was also apparent. On leaving the nest the male did not fly into the undergrowth but often sat on an exposed perch near the nest and sang loudly. The difference in the fantail's behaviour from the general trend apparent in other passerines suggests that conspicuousness of the fantail around the nest does not impose a threat to the parents, nest, eggs or young. Such behaviour is understandable if the fantails' predators hunt with the eyes or nose rather than with their ears. However, not enough information on the predators of the South Island Fantail is available to substantiate this conclusion.

Many aspects of the incubation behaviour of the South Island Fantail appear to be non-adaptive, persisting because they do not decrease reproductive efficiency.

CHAPTER 7

CHAPTER 7

PARENTAL CARE

7.1 INTRODUCTION

Parental care encompasses the protection, feeding and general care of young by one or both parents from the time of hatching to independence (Thomson 1964).

7.2 METHODS

Parental care of six broods by three pairs was studied. Because two broods were deserted (Table 1), results during the fledgling stage were based on four broods.

Three important factors must be borne in mind when assessing the following results:-

(i) seventy-seven per cent of the 14 nests were too high to yield information on the day and time of hatching and on the size of the brood. Knowledge of the brood size is essential for explaining differences in feeding rates between broods.

(ii) quantitative results were only obtained during my standard observation period of 0900h to 1700h, and variations in feeding frequency due to early morning and late evening conditions were not investigated, and

(iii) a quantitative study of food brought to the nest and to fledglings was not attempted because of the difficulty in identifying number and types of food items carried in the parent's beak. Elaborate apparatus is required to obtain

TABLE 23. Number of visits per hour to the nest during the nesting stage.

Day*	Nest 5				Nest 13			
	Number of one hour observation periods	Mean number of visits/h			Number of one hour observation periods	Mean number of visits/h		
		Female	Male	Total		Female	Male	Total
1	3	10	6	16	-	-	-	-
3	3	12	14	24	-	-	-	-
5	4	9	11	20	-	-	-	-
6	-	-	-	-	3	5	4	9
7	3	17	14	31	-	-	-	-
8	1	15	13	28	2	8	9	17
9	-	-	-	-	-	-	-	-
10	-	-	-	-	2	17	14	31
12	-	-	-	-	2	24	12	36
14	-	-	-	-	2	21	16	28
16	-	-	-	-	2	26	20	46

* Day 1 is the day the young hatched. This was 27/9/75 for Nest 5 and 3/11/75 for Nest 13.

information on this aspect. Royama (1966) automatically photographed each item brought to the nest by Great Tits *(Parus major)*. The kind and size of food were determined by examining the film under a microscope. Such apparatus was not available for this study.

Because of these factors the data presented in the following section do not provide a detailed study of parental behaviour by the fantail.

7.3 RESULTS

7.3.1 Hatching

Hatching probably takes place on the 13th or 14th day of incubation. However, the exact time of hatching was not determined because nests could not be observed closely. The parents showed a marked change in behaviour the day hatching was assumed to have taken place. Before hatching, the parents settled into the nest quietly but after hatching they gave a large amount of "Feeding vocalisations" and pivoted on the nest-rim before settling. On the 13th or 14th day of incubation a parent frequently delved deep into the nest bowl, then raised its head and appeared to swallow something, probably faecal pellets or the eggshell. The activity was very similar to that used in drinking. I often observed a white substance (possibly uric acid) on the bird's bill.

I did not observe fantails carrying away eggshells, nor found eggshell fragments around the nest.

7.3.2 Feeding Nestlings

Both sexes fed the young, apparently with equal frequency (Table 23). Because of a lack of information on quantities of food taken to the nest it was impossible to determine whether one individual provided more food than the other.

The number of parental visits to the nest per hour increased after hatching. One pair made an average of six visits per hour to Nest 5 during the incubation period, 16 visits per hour after hatching, and 28 visits per hour just before fledgling. The same trend was apparent in P2R at Nest 13 (Table 23).

There appeared to be a general increase in the feeding frequency during the nestling stage (Table 23). Although this trend was apparent at Nest 5 and Nest 13, the rate at which the feeding frequency increased differed between nests. By day eight the number of visits per hour had increased to 28 at Nest 5 but only 17 at Nest 13.

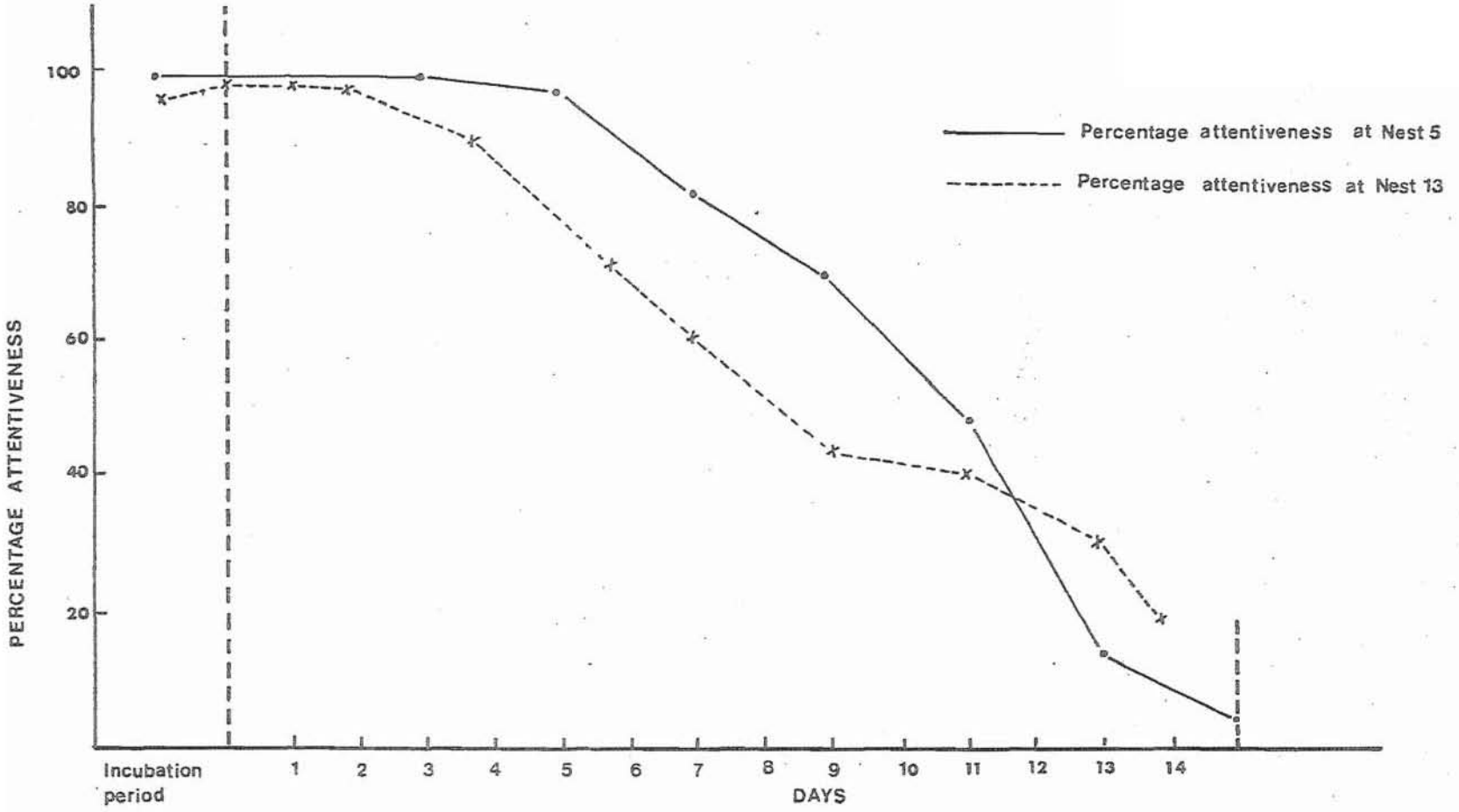
After catching and subduing prey (usually blowflies) one to eight metres from the nest, the parents carried them to the nestlings. The food was sometimes dropped and recaught during the flight.

Once on the nest rim the parent usually stood pivoting, "Tail flashing" (Section 12.4.2) and gave a soft "Feeding vocalisation" (Table 24). The bird gave the vocalisation in 79.5% of 58 observations, but pivoting occurred slightly less frequently, 68% (n = 58). A similar vocalisation was presumably noted by Roberts (1942) when studying the Willie Wagtail: "the well-fed nestlings were sometimes indifferent to food but a chattering note uttered by the parent bird at the nest acted as a stimulus". After feeding, the fantail either flew away or settled to brood.

TABLE 24. Behaviour exhibited by parents before feeding nestlings.

Behaviour	Number of observations	Percentage frequency
Standing quietly	4	7
"Feeding vocalisation" only	16	27
"Feeding vocalisation" and "pivoting"	30	52
"Pivoting" only	8	14
Total	58	100

FIGURE 10. Percentage attentiveness during the nestling period.



see Table 25

7.3.3 Brooding

Brooding refers to the action of sitting on the young, usually in the nest, to keep them warm (Thomson 1964).

For at least two days after hatching nest attentiveness was high (Table 25) but by the fourth day less time was spent brooding and more time collecting food for the nestling. By the ninth day the attentiveness had dropped a great deal (Fig. 10).

TABLE 25. Percentage attentiveness between 0900 - 1700h during the nestling stage.

Day	Nest 5		Nest 13	
	Percentage attentiveness	Length of observation period (min)	Percentage attentiveness	Length of observation period (min)
1*	96	124	98	145
2	99	116	99	177
3	98	149	-	-
4	-	-	-	-
5	88	209	-	-
6	-	-	100	180
7	69	167	-	-
8	59	200	97	201
9	57	60	-	-
10	-	-	83	160
11	40	150	-	-
12	-	-	70	153
13	30	123	-	-
14	17	99	49	160
15	-	-	-	-
16	deserted		13	166
17			4	137

*Day 1 and 2 refer to the two days before hatching.

Both sexes share brooding equally at the start of the nestling stage, but most is done by the female as the chicks get older (Table 26).

The length of the average brooding spell was seven minutes (in P2R and P2B) but the range was wide, i.e., 0.5 to 30 minutes. There was no obvious difference in the length of spells either between the sexes or from day-to-day (Table 27).

TABLE 26. The role of the sexes in brooding.

Day	Nest 5			Nest 13		
	Time spent observing brooding behaviour (min)	Percentage of time female spent brooding	Percentage of time male spent brooding	Time spent observing brooding behaviour (min)	Percentage of time female spent brooding	Percentage of time male spent brooding
1	149	59	41	-	-	-
2	-	-	-	-	-	-
3	209	73	27	-	-	-
4	-	-	-	180	55	45
5	167	86	14	-	-	-
6	200	78	22	201	60	40
7	60	68	32	-	-	-
8	-	-	-	160	63	37
9	150	100	0	-	-	-
10	-	-	-	153	60	40
11	123	91	8	-	-	-
12	99	95	5	160	74	26
13	-	-	-	-	-	-
14	-	-	-	166	89	11

Because the percentage attentiveness decreased during the nestling stage but the length of the brooding spells remained the same, the number of brooding spells must decrease from day-to-day. This is due to increasing demands on the parents for food, allowing less time to brood. It is important to note that the fantail does not spend shorter periods, but fewer periods brooding. I suspect that once in the nest the bird responds instinctly by staying there for a specific length of time.

TABLE 27. Length of brooding spells.

	Nest 5		Nest 13	
Day	Length of female's brooding spell	Length of male's brooding spell	Length of female's brooding spell	Length of male's brooding spell
1*	$\bar{X}$ = 10 R = 1-17 n = 11	$\bar{X}$ = 7 R = 2-12 n = 13	$\bar{X}$ = 8.5 R = 1-16.5 n = 11	$\bar{X}$ = 8.5 R = 6-16 n = 9
3	$\bar{X}$ = 6 R = 1-31.5 n = 14	$\bar{X}$ = 4 R = 0.5-12 n = 9	$\bar{X}$ = 7.5 R = 0.5-15 n = 10	$\bar{X}$ = 7 R = 0.5-12 n = 11
4	$\bar{X}$ = 7 R = 2-11.5 n = 14	$\bar{X}$ = 5 R = 0.5-13 n = 3	—	—
5	—	—	$\bar{X}$ = 3.5 R = 0.5-12 n = 19	$\bar{X}$ = 4 R = 0.5-8 n = 9
7	$\bar{X}$ = 5 R = 0.5-16 n = 8	$\bar{X}$ = 6 R = 1-16 n = 3	$\bar{X}$ = 8 R = 1-25 n = 8	$\bar{X}$ = 10 R = 1-17 n = 5
9	—	—	$\bar{X}$ = 5 R = 1-33.5 n = 11	$\bar{X}$ = 5 R = 1-11 n = 4

$\bar{X}$ = mean length of brooding spell, R = range of brooding spells, n = number of brooding spells.
* Day 1 for Nest 5 is 27/9/75 and Nest 13 is 6/11/75.

While brooding, the parent often lifted itself up, probed into the nest (probably to reposition the chicks) and resettled. Behaviour during nest-relief was much the same as during incubation, i.e. "Type 1"

calls and "Aerial displays" by the approaching fantail, and stretching or preening by the bird leaving the nest (Section 6.3.6).

I obtained no information on diurnal variation in attentiveness.

7.3.4 Nest Sanitation

At four nests, both sexes removed faecal pellets with approximately equal frequency (Table 28) after Day 2 of the nestling stage.

TABLE 28. The role of the sexes in nest sanitation.

Nest	Number of faecal pellets removed			Percentage frequency of faecal pellets removed		
	By the female	By the male	Total	By the female	By the male	Total
5	60	54	114	52	48	100
6	99	111	210	47	53	100
13	41	49	90	45	55	100

A parent would wait on the nest for several seconds, pick up a pellet and drop it during the flight away from the nest. Because a bird usually flew to the same perch the pellet was generally dropped at the same place, one to two metres from the nest. On landing the bird gave "Type 2" vocalisations, "Bill-wiped" and either flew away or returned to the nest (Table 29).

TABLE 29. Frequency of flights back to the nest, or away from it, after removing faecal pellets.

Nest	Number of observations			Percentage frequency of observ.		
	Returned to the nest	Flew away	Total	Returned to the nest	Flew away	Total
5	25	16	41	64	34	100
6	19	21	40	47	53	100
12	35	25	60	59	41	100
13	9	13	22	41	39	100

7.3.5 Feeding of Fledglings

The young were fed by both parents throughout the fledgling stage. Loud "Type 1" calls given by approaching parents stimulated wing vibrations and a "Buzzing" vocalisation (i.e., food-begging) in the young. The parents appeared to feed each chick equally, often hopping over the backs of several chicks to reach one on the other side of the group.

By the sixth day the young tended to approach the parents for food. This "excited" the parents and elicited a sudden increase in "Type 2" vocalisations, and a refusal to feed the young was noted. By the eighth day the parents approached but rarely fed the fledglings who had started hawking (clumsily) and catching moths.

The second nest was often begun while the parents were still feeding the previous brood. The female did most of the building, and consequently, less feeding.

7.3.6 Protection of Fledglings

The male frequently attacked thrushes and silvereyes in the nest-site. When the parent started pecking and giving "Type 2" vocalisations (during the attack) the young quickly moved apart and sat quietly in the foliage. The female often sat close-by, but occasionally helped with the attack.

7.4 DISCUSSION

Parental care by the South Island Fantail resembles that exhibited by parents of other passerine species.

Most of the nests were too high to obtain information on the exact time of hatching and response of parents to the activity of hatching or recently hatched young. However, hatching was assumed to

have taken place on the day the parents displayed a marked change in behaviour at the nest. The parents landed on the nest and quietly "settled" on the eggs during incubation. On the 13th or 14th day of incubation the parents pivoted and gave a "Feeding vocalisation" for several seconds after landing on the nest. They also appeared to swallow eggshell fragments (Section 7.3.1). Many passerines eat or remove eggshells from the nest. I never observed fantails carrying away egg-shells, nor found fragments in the nest-site. Therefore I suspect that the South Island Fantail eats the eggshells. It should be borne in mind that this conclusion is based on observations at six nests and further observations may find these results to be atypical for the species. Information on differences in the behaviour of the sexes during hatching, particularly with respect to the disposal of eggshells, was not obtained. It is possible that the female fantail alone eats eggshells to obtain calcium, which she may have become deficient in as a result of egg-formation. However, more work is required on this aspect.

As soon as the young emerge from the shell, young birds are brooded by the parents to dry their down, if they have any, and to warm and shelter them against the elements (Welty 1962). Brooding is fundamentally a continuation of incubation behaviour through the early stages in the development of the young, consequently "nest attentiveness" is very high. At Nest 5 the per cent attentiveness during the first three days of the nestling stage resembled the degree of attentiveness during incubation (Fig. 10). The high "nest attentiveness" during the early stages of nestling period is probably an instinctive and adaptive response by the parents to the presence of cold-blooded or poikilothermic young. The daily decrease in the time devoted by the parents to brooding (after day three of the nestling stage - Section 7.3.3) is probably closely adapted to the gradual development of temperature

control by the young. Pettingill (1970) noted that the amount of brooding given to the young depends on several factors, including the rapidity with which young develop body-temperature control, climatic conditions, and protection of the nest. The slower rate of decrease in "nest attentiveness" at Nest 13 (Section 7.3.3) could have been due to cooler or wetter weather conditions. In other passerines excessively cool weather, heavy rains, or exposure of the nest to intense sunlight may prolong or cause a return of brooding (Van Tyne and Berger 1966).

In many passerines the participation of the sexes in brooding is the same as in incubation (Van Tyne and Berger 1966). This was not the case in the fantail. The female and male shared incubation equally, but during the nestling stage "nest attentiveness" (i.e., brooding) by the male decreased daily (Table 7.4). The tendency for the female to spend more time brooding than the male, and for the male to spend more time feeding the young, is probably partly due to an instinctive response but also due to experience. The female has more experience incubating (or sitting on the nest) during the night rest and during the first few days of the incubation period of the second and third broods. However the male has more experience feeding other nestlings, fledglings and his mate.

In the South Island Fantail both sexes share in the feeding of the nestlings. In passerine species the rate of feeding increases daily because of the increasing needs of fast-growing young (Wolfson 1955). A daily increase in feeding frequencies was evident in this study (Section 7.3.2). The difference in the rate of increase in the feeding frequency at Nest 5 and Nest 13 could be due to weather conditions or, more likely, to the number of young. Royama (1960) found that the feeding frequency was greater in larger clutches (compared with smaller ones) because of higher demands for food by a larger number of young.

Because the nests were too high to obtain information on the size of the clutch it is impossible to determine whether or not clutch size caused a change in the rate of feeding.

Unlike many passerines, the South Island Fantail removed faecal pellets by carrying and dropping them during a flight away from the nest, rather than by eating them. Wallace and Mahan (1975) noted that food passing through the very young nestlings still retains some undigested remnants which may provide nourishment for the parent bird who is often too busy to seek food for itself. It is very likely that the eating of faecal pellets is a response to high demands on the parents for food, as well as to a low availability of food. An abundance of prey during the South Island Fantails' breeding season may not have warranted this adaptation.

The fact that the fantail always dropped faecal pellets at the same spot, approximately 1.5 metres from the nest, suggests that conspicuousness of the nest-site does not impose a danger to the young or to the species.

The parents continued to feed the young (fledglings) once they left the nest. By the eighth day the parents started to "refuse" to feed the "begging" young. This "refusal" is probably a naturally evolved device to encourage the young to seek their own food.

The parents appeared to be particularly aggressive towards other passerines in the nest-site during the nestling and fledgling stage (Section 11.3.1). Responses to potential predators were not observed.

CHAPTER 8

CHAPTER 8

MAINTENANCE BEHAVIOUR AND COMFORT MOVEMENTS

8.1 INTRODUCTION

In this chapter I describe a number of maintenance activities, i.e., activities essential to the life, repair and general efficiency of a bird (or animal). They include bathing, resting, drinking and feather care. Feeding, the most important maintenance activity, is discussed in Chapter nine.

8.2 METHODS

One hundred and twelve observations of preening activities and 89 observations of comfort movements were made. Twenty-two preening sequences were recorded on a tape-recorder. By using abbreviated terms to record the area of the body preened it was possible to make a detailed study on the sequence of the preening movements. Each time the bird lifted its head during the sequence I noted the area of the body where the bill was repositioned.

8.3 RESULTS

8.3.1 Feather Care

Feather care is a term covering a range of highly stereotyped basic movements, together with associated behaviour. "The major patterns of feather maintenance include true bathing, oiling, preening and head scratching; sunning, dusting and anting are subsidiary ones" (Thomson 1964).

8.3.1a Preening

Preening activities occurred throughout the day and year, and comprised the "arrangement, cleaning, and general maintenance of the health and structure of the feathers by the bill" (Thomson 1964).

Preening bouts were classified on the basis of the behaviour associated with each type, the length of the bout, and the form of the behavioural activities. Three types were identified and included:-

(i) extended preening bouts. Long preening bouts of up to 20 minutes occurred after bathing and during inactive periods. These bouts, which involved up to 180 movements, were occasionally interrupted by hawking forays or song bouts. Extensive preening of all areas of the body characterised this type,

(ii) temporary preening bouts. These were of short duration (4-10 secs) and involved fast preening movements of two or three areas of the body. Temporary preening was particularly evident after nest-building, nest-relief, "Hop-over" displays and foraging, and

(iii) displacement preening was characterised by very rapid and short preening movements and was given in situations where the motivation to preen should have been low, e.g., when I approached or made a lot of noise around a bird. Andrew (1956a) noted that displacement preening is given in conflict situations because a weak tendency to give it is overtly expressed at moments when two strong tendencies to give responses incompatible with each other (e.g., curiosity and fear) balance.

Preening movements during these bouts were of two kinds: "Nibbling" and "Drawing". When "Nibbling", the birds seized feathers in the tips of the mandibles and passed them between the mandibles repeatedly, working from the base to the tip. This method was commonly

TABLE 30. Extended preening sequences.

PRECEDED BY ↓ / Areas preened	FOLLOWED BY → Chest	Jugulum	Under 1st wing	Under 2nd wing	Top 1st wing	Top 2nd wing	Back 1st wing	Back 2nd wing	Foot	Top tail	Back	Scratch, Shake, Stretch
Chest	141*	15	14	6	10	8	10	5	4	3	13	4
Jugulum	15	24*	3	3	1	0	1	1	0	4	1	3
Under 1st wing	14	1	25*	6	15	1	7	5	0	4	1	7
Under 2nd wing	5	1	4	9*	1	3	2	7	0	3	1	3
Top 1st wing	14	3	8	2	38*	3	3	1	2	6	5	6
Top 2nd wing	7	2	2	2	5	17*	1	2	1	1	1	1
Back 1st wing	6	1	12	1	6	3	13*	4	0	1	3	0
Back 2nd wing	4	2	7	2	1	0	6	20*	0	0	0	3
Foot	1	0	0	1	1	1	1	0	4*	0	0	2
Top tail	4	3	6	3	6	2	3	0	0	20*	6	1
Back	9	1	4	2	2	4	1	1	0	4	30*	6
Scratch, Shake	7	3	1	2	5	1	2	4	0	8	3	0*

* Indicates a relationship between areas of the body preened. For example, preening of the chest was usually followed by preening of the chest. The preening of the top of the first wing was usually followed by preening movements at the top of the same wing.

employed when preening the breast, jugulum and around the wings. "Drawing" was similar to "Nibbling" but the bird pulled the feather through the bill in one movement. These "Drawing" movements separated individual rectrices as single feathers were pulled through the bill.

An investigation of 22 extended preening bouts (Table 30) indicated:-

(i) a large amount of chest preening,

(ii) a tendency to preen the same area repeatedly, and

(iii) a tendency to preen around the wing, i.e., preening under the wing was usually followed by preening behind and at the top of the same wing.

8.3.1b Bathing and Drying

Fantails bathed in streams and puddles throughout the year. They stood 12 to 24 centimetres from the water's edge or on small branches 20 to 30 centimetres above the stream. On many occasions (n = 20) I watched a bird hop into the water giving many loud "Fast type 1" calls. Once in the water the fantail crouched and dunked its head which was lifted as the body was lowered further into the water. While crouched in the water the tail was lowered from 60° above the horizontal to the horizontal position and flicked rapidly from side-to-side as the wings were flicked upwards from the body. After these movements, the fantail hopped out of the stream and gave "Type 1" calls before landing on a nearby perch. Here the bird performed active drying movements which included feather ruffling and intensive tail shaking. After a short period the fantail returned to the stream and repeated the activities. The bird re-entered the water as many as 30 times during a single bathe.

8.3.1c Sunbathing

Hauser (1957) characterised voluntary sun-bathing by a fluffing

out of the bird's feathers, an immobile pose, followed by ruffling and preening. Such sequences of activities were observed in the fantail. More intensive sunbathing activities were noted on two occasions. Once the bird moved from the shade to an exposed perch and sat at right angles to the sun, the wing and half the tail (that was nearest to the sun) extended, and head turned away from the sun. The fantail sat for two minutes in this position before returning to a shady area to continue preening. On another occasion the bird sat on the nest with the tail and both wings fully extended for one or two minutes.

Involuntary sunbathing (or "Compulsory responses" to the sun, Hauser 1957) was not identified although its presence could exist.

8.3.2 Comfort Movements

Comfort movements are movements that aim to make the bird more comfortable. A description of some comfort movements and the behaviour relevant to the care of soft parts follows.

8.3.2a "Bill-wiping"

"Bill-wiping" started with an initial lowering of the head below the level of the branch. As the head was raised the bill was drawn (from base to tip) against the side of the branch. The bird immediately repeated the movements in 82% of 111 observations. Long episodes of "Bill-wiping" occurred, during which the bird turned on the perch to wipe the beak (against the branch) on both sides of the body.

"Bill-wiping" was of two types:-

(i) functional bill-wiping. This occurred after courtship feeding, nest-building, devouring prey, feeding nestlings and removing faecal pellets. It removed dirt or foreign particles from the bill, and

(ii) displacement bill-wiping. This was observed after chases and during aggressive interactions with conspecifics.

8.3.2b Head Scratching

There are two main ways in which birds bring the foot up to the head and bill for scratching: "directly" and "indirectly". When scratching indirectly the bird lowers one wing and brings the corresponding leg over the shoulder to the head. When scratching directly it simply brings the foot straight up to the head without first making the special movement of the wing (Simmons 1961).

The South Island Fantail scratches directly, although most passerines use the indirect method. I could not find any information on scratching in any other *Rhipidura* species.

Direct head-scratching by the fantail could be further classified.

(i) Rapid scratching occurred momentarily as the bird stopped foraging, stood up in the nest, or after nest-relief. Simmons (1961) termed this "Basic scratching", which "is an automatic response to irritation or foreign bodies on the head". The exact cause of scratching in this study is not known.

(ii) By "Extended scratching" I refer to long bouts of scratching, often given in the preening sequence. Both feet were used, first one, then the other.

8.3.2c Stretching

Two types of stretching movements occurred and involved:-

(i) the extension of one wing and corresponding leg. The leg was extended backwards and held up under the tail, which was fanned on that side. This type occurred in 55% of 41 observations of stretching, and

(ii) an upward stretch of both wings simultaneously. There was very little wing extension and no tail spread. It accounted for 45% of the observations.

Occasionally, stretching of one side of the body was followed by a

stretching of the other side, or by an upward stretch of both wings.

Stretching occurred frequently after long rest periods or spells on the nest. It was usually followed by tail fanning and subsequent foraging activities or flights away from the nest.

8.3.2d "Face-rub"

The base of the bill was placed against the side of a branch during the "Face-rub". The head was slowly rotated (once or twice), rubbing an area between the eye and bill against the perch.

This activity, which was not observed frequently, occurred during preening bouts, nest-building and after nest-relief. It may be a response to an irritation of the face or eye.

8.3.2e "Head-forward"

"Head-forward" movements occurred during incubation and brooding. Fantails often stood up in the nest to preen or to rearrange eggs and nestlings. On resettling, the neck was rapidly extended and relaxed. These movements were observed (less frequently) after stretching and "Courtship feeding".

8.3.2f "Yawning"

The bill was opened wide in this stretching or "Yawning" movement and occurred during "Nest attentiveness".

8.3.2g Pecking

The fantail occasionally pecked vigorously at its leg or foot afer leaving the nest and during preening bouts. It appeared to be a response to some irritation.

8.3.3 Drinking

Fantails occasionally (n = 8) drank from the stream, ponds and puddles. A bird would stand on the water's edge, lower its beak into the water and then raise its head to a vertical position. The same movements were made by birds drinking from raindrops adhering to foliage.

8.3.4 Resting

In resting attitudes the head was withdrawn on the shoulders (but not turned), the contour feathers were raised, the tail closed and slightly depressed, the wings were tucked tightly together above the tail and the legs were flexed. The bird often stood on one leg, tucking the other into the feathers.

In the full sleeping attitude the head was withdrawn and turned so that the bill rested in the shoulder feathers.

These attitudes were observed during mid-day and late-afternoon rest periods. Although I did not locate birds at night, these attitudes probably exist during the night-rest period.

8.4 DISCUSSION

The types of preening bouts and movements resemble those of other passerines (Gibb 1947, Andrew 1956a, Brockway 1963, Thomson 1964, Pettingill 1970). The large amount of chest preening noted in the 22 extended preening bouts could be attributed to the method of scoring the areas preened and number of preening movements, i.e., every time the head was lifted and placed back towards the body a score was taken. When preening the chest, the bird tended to quickly "Nibble" or "Draw" feathers, repeating these movements many times. However, when preening other parts of the body, I suspect that just as much time was spent preening but head lifting was less common. Because of problems encountered in timing preening sequences, detailed information on this aspect was not obtained. The fact that the fantail tended to preen the same area repeatedly and preen around the wing suggests that more efficient maintenance probably occurs when preening is localised to specific areas.

In many species, bathing birds "are particularly vulnerable to

predation; their movements are conspicuous and their flying efficiency is reduced; they need at any stage in the bathing process to be able to escape from sudden attack" (Thomson 1964). The fact that the most characteristic behaviour associated with bathing in this study was large numbers of "Fast type 1" calls (a distress and alarm call) suggests that this activity is a potentially dangerous one for the species. However, the fantail's bathing behaviour encompasses a number of adaptations that may have counteracted the threat imposed by predators. They included:-

(i) the "In-out" bathing tactics. Because fantails did not spend long periods in the water they were only vulnerable for short periods,

(ii) the fact that drying activities were performed in dense foliage where the fantail's conspicuousness was greatly reduced, and

(iii) a tendency to bathe with small groups of silvereyes and conspecifics. This could have two functions. Firstly, a fantail bathing with a large group of silvereyes is less likely to be caught by a predator than if it had been the only bird present. Secondly, the fantail may benefit from the silvereyes' sense of danger; the silvereyes appear to be particularly sensitive to any sound or movement in the bush.

Sun-bathing was evident in the fantail. There is some controversy as to the function of sun-bathing but the most popular hypothesis include:-

(i) the removal of parasites. It is possible that the heat from the sun may cause ectoparasites to become more active. This stimulates scratching and the possible removal of parasites, and

(ii) the conversion of oils into Vitamin D (Yapp 1970).

These functions probably act in the fantail.

Comfort movements in the fantail are similar to those of other

species of passerines (Nice and Schantz 1959a, Simmons 1961, Brockway 1963, Thomson 1964).

CHAPTER 9

CHAPTER 9

FEEDING BEHAVIOUR

9.1 INTRODUCTION

The areas searched during foraging, and methods of prey capture, are recorded. An account of prey manipulation, feeding associations with other passerines, and seasonal variation in prey capture by the South Island Fantail completes this chapter.

9.2 METHODS

Repeated standard observations, similar to those employed by Gibb (1954) when studying titmice, were taken daily from March 1975 to March 1976. A total of 1532 feeding observations, recorded between 0900h and 1100h, included information on the nature of the bird's activity when first seen, the feeding level and feeding method used by the fantail.

In this study I refer to six feeding levels. They are:-

(i) the canopy, the uppermost storey of tree crowns, unshaded by other crowns 6-15 metres above the ground,

(ii) the upperstorey, a storey of plant crowns shaded by the canopy, 3-6 metres above the ground,

(iii) the middlestorey, 1.5 to 3 metres above the ground,

(iv) the lowerstorey, 0.5 to 1.5 metres above the ground,

(v) a level "just above the ground" (0 to 0.5 metres), and

(vi) the ground level.

A 16mm cinefilm was used to obtain detailed information on

feeding methods. However, because of the low light intensity in the bush and very quick movements by the fantail, very few results were obtained. The cinefilm was taken at a speed of 25 frames per second and sketches were obtained from a frame-by-frame analysis of the film.

Although errors may have occurred as a result of:-

(i) biases towards stations at the lower levels, where visibility is better,

(ii) observations being confined to a specific period of the day, and

(iii) the impracticality of recording the exact time spent feeding at each level,

the quantitative data support the trends apparent during daily observations.

9.3 RESULTS

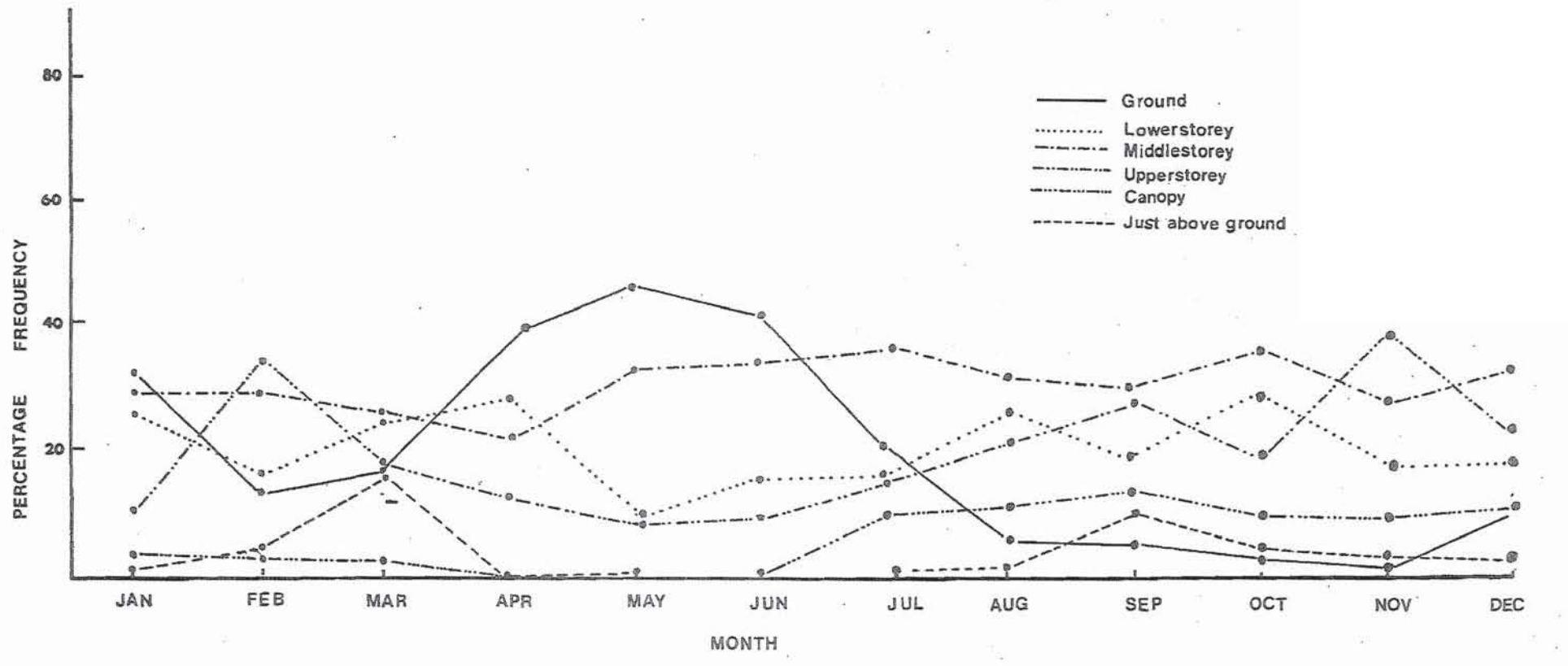
9. 3.1 Use of the Foraging Levels while Feeding

The fantails spent significantly more time feeding in the branches (χ^2 = 1326, df = 1, $p > 0.001$), although 17% of 1532 feeding observations occurred on the ground. Fantails fed within 0.5 metres of the ground and between six and 15 metres, but the frequency was small compared with preferences for other feeding levels (Table 31).

TABLE 31. Use of the foraging levels.

Foraging level	Number of observations	Percentage frequency of observations
Ground	262	17.0
Just above the ground	44	3.0
Lowerstorey	314	21.0
Middlestorey	470	31.0
Upperstorey	330	21.0
Canopy	112	7.0
Total	1532	100.0

FIGURE 11. Seasonal variation in the use of different feeding levels.



Seasonal variation in the use of different foraging levels was apparent. In the winter months (April to July) a preference for ground feeding and foraging in the middlestorey was apparent, and very little feeding within 0.5 metres of the ground or at heights greater than six metres occurred (Table 32, Fig. 11).

As the breeding season commenced (August) there was a decrease in ground feeding and an increase in foraging in the lowerstorey, upperstorey and canopy, but the frequency of feeding in the middlestorey remained the same. Foraging within 0.5 metres of the ground increased slightly.

As the breeding season ended (December) the amount of feeding in the lower, middle and upperstorey remained constant but feeding at heights above six metres decreased and ground feeding increased. At the onset of winter, feeding on the ground and middlestorey increased further and there was a slight drop in lower and upperstorey foraging.

9.3.2 Methods of Prey Capture

The South Island Fantail used five feeding methods:-

(a) "Active canopy feeding",

(b) "Hawking forays",

(c) "Aerial feeding",

(d) "Ground feeding", and

(e) "Tree-trunk feeding".

A description of each method follows.

9.3.2a "Active canopy feeding"

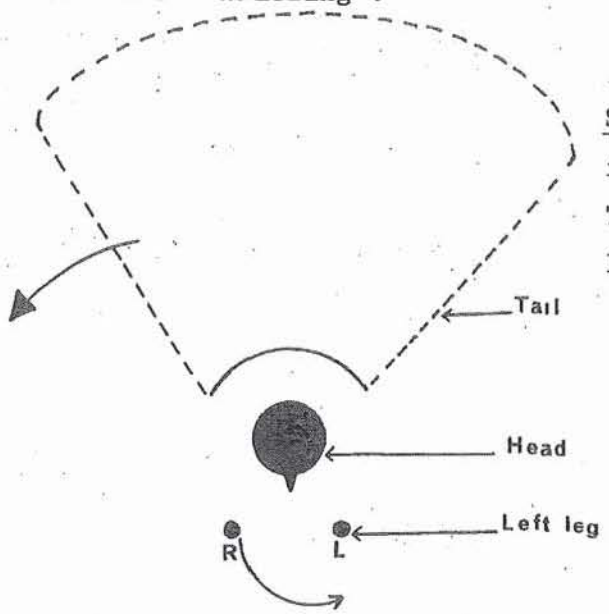
By "Active canopy feeding" I refer to the activities that a bird engages in when actively seeking out its prey from the branches rather than waiting for the appearance of the prey (tactics characteristic of "Hawking forays" and "Aerial feeding" - see Sections 9.3.2b and 9.3.2c).

TABLE 32. Seasonal variation in the use of the feeding levels.

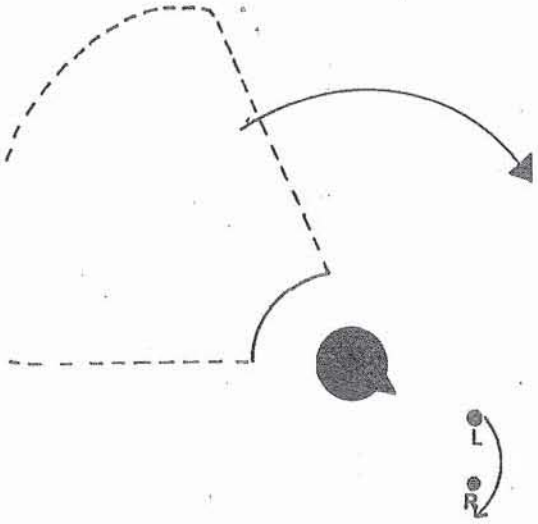
Month	Number of observations						Percentage frequency of observations					
	Ground	Just above ground	Lower-storey	Middle-storey	Upper-storey	Canopy	Ground	Just above ground	Lower-storey	Middle-storey	Upper-storey	Canopy
March	10	8	15	16	11	1	16	13	25	26	18	2
April	55	0	41	32	17	0	38	0	28	22	12	0
May	117	1	25	83	22	0	47	0	11	34	9	0
June	13	0	5	11	3	0	41	0	16	34	9	0
July	4	0	3	7	3	2	21	0	16	37	16	11
August	13	4	53	65	44	24	6	2	26	32	22	12
September	10	6	36	57	52	27	5	3	19	30	28	14
October	6	6	56	71	37	20	3	3	29	36	19	10
November	2	12	40	63	85	22	1	5	18	28	38	10
December	10	3	17	30	22	12	11	3	18	32	23	13
January	10	0	8	9	3	1	32	0	26	29	10	3
February	12	4	15	26	31	3	13	4	16	29	34	3

PLATE 1. The body posture of the fantail when foraging.

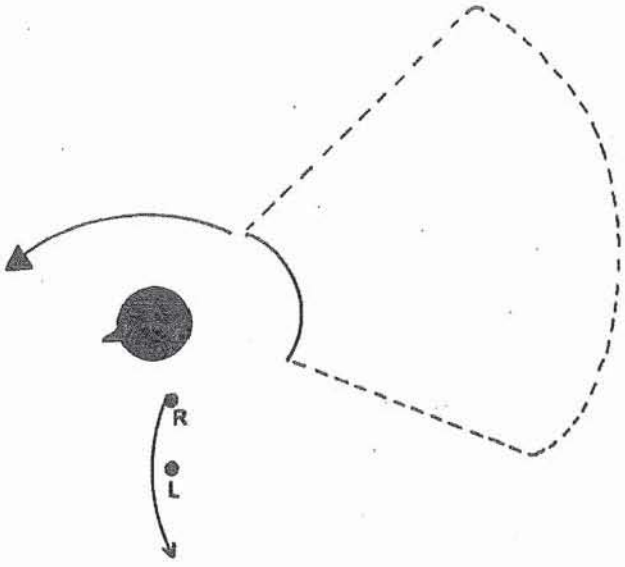
FIGURE 12. "Waltzing".



Step 1: Bird steps forward with right leg. Tail swings to bird's left.



Step 2: Left foot is brought directly in front of right foot. Tail swings 180°.



Step 3: Right foot is brought directly in front of left. Tail swings back 180°.

While moving along branches the fantails affected a characteristic posture. The tail was completely fanned and positioned 0^{o} to 45^{o} above the level of the back, while the wings were slightly spread and drooped (Plate 1). In this attitude the bird walked along the branch alternately moving each foot so that one was placed approximately five centimetres in front of the other. These movements, which I have termed "Waltzing", caused the body to be twisted through 90^{o} (Fig. 12). The mean number of strides in 131 fifteen second intervals equalled eight. The bird occasionally stopped and rapidly cocked its head from side-to-side as it "Waltzed" along the branch.

Movement from branch to branch or tree to tree was accomplished by:-

(i) hopping. Before each hop the tail (which was fanned) was flicked to a position 90^{o} with respect to the body. The legs were folded, breast lowered, head and neck withdrawn, the wings raised and held away from the body,

(ii) slow, gliding flights with tail and wings fanned, or

(iii) fast, flapping flights with a closed tail.

When moving through closely intertwined vines the head was lowered and rectrices tightly closed. This posture appeared to assist movement through the vines, from which the bird often darted out to snap insects disturbed by the movement.

Some prey were pecked off trunk surfaces as the fantail hopped up small branches close to the trunk. Before each hop (to a branch directly above the bird) the fanned tail was flicked from a horizontal to a vertical position. The tail was lowered during the hop. On landing, the bird leaned forward and pecked at crevices in the trunk.

Fantails also clung upside-down on the underside of branches and foliage. After landing on a branch a bird sometimes swung forward or backwards, so that it lay upside-down with tail and wing fanned.

However, on most occasions the bird landed on the underside of the branch in the upside-down position. From this position the bird released itself, flipped over as it darted down to snap passing prey and glided to a nearby branch. Fantails can right themselves after falling less than five centimetres. They were never observed walking upside-down.

The most common means of "Active canopy feeding" between December and April consisted of "Tumbling flights" through the foliage. Because the bird was often hidden by the foliage a detailed description is difficult to make. However, the bird appeared to fall through the foliage fluttering its wings a great deal. Small insects and moths disturbed by the "Tumbling flights" were caught in the lowerstorey or just above the ground.

9.3.2b "Hawking forays"

"Hawking forays", which involved fast direct flights from a perch to catch passing insects, was the main method employed in the breeding season (Section 9.3.1). While perched between flights the bird pivoted (at a mean rate of three turns per second - Section 12.4.2), and the rectrices flicked out. The intensity of body pivoting appeared to be correlated to the bird's motivation to feed, i.e., a large amount of pivoting appeared to coincide with a large number of flights during a single bout of hawking forays. Quantitative data on this aspect were not obtained because of the difficulty I encountered in obtaining cinematographic information.

Hawking flights were either slow "Fluttering flights" or "Rocketting" ones. "Fluttering flights" incorporated wing and tail fanning during turns and occasional acrobatic manoeuvres. "Rocketting" involved fast direct flights and were used to capture fast flying insects such as blowflies *(Calliphora erythrocephala)*.

Sixty-six per cent of 65 hawking flights were directed downwards (Table 33). The tendency to fly down and to one side rather than down to catch prey ($\chi^2 = 93$, df = 1, $p > 0.001$).

TABLE 33. The direction of hawking flights.

Direction of flight with respect to the fantail	Number of observations	Percentage frequency of observations
Down	43	66
Up	5	8
To one side	17	26
Total	65	100

The mean length of a hawking manoeuvre was one second with a range of 0.5 to three seconds (Table 34). The range was a result of a number of factors which included the type of flight (i.e., "Rocketting" flights were usually faster than "Fluttering flights") and the distance the fantail had to fly to catch its prey. Fantails caught insects two to 15 metres from the perch.

Small prey were usually swallowed in flight but large prey were brought back to the perch and further subdued before eating it (Section 9.3.4). Before landing, the tail and wings were fanned and the body brought from a horizontal to vertical position to assist braking and landing. After eating the prey, the bird turned (with a single hop) and resumed its pivoting and scanning tactics. The mean time perched between successive flights of a hawing bout equalled three seconds (Table 34).

Although the bird returned to its original perch after 30% of 65 observations of hawking flights, it usually (70%) landed on a branch directly in the line of strike. The fantail resumed its hawking

activities from that perch or flew directly back to theoriginal perch.

Hawking flights occurred in all parts of the bush, from fallen logs (five centimetres off the ground) to heights of 12 metres.

TABLE 34. Time between successive "Aerial" flights and "Hawking forays".

Mean length of time between "Aerial" flights	= 17.5 s
Range	= 2.0 - 39.6 s
Number of flights recorded	= 118
Mean length of time between "Hawking forays"	= 3.6 s
Range	= 0.6 - 13.2 s
Number of forays recorded	= 30
$t = 3.5$, df = 46, $p > 0.01$, Appendix 6	

3.3.2c "Aerial Feeding"

Aerial feeding differed from hawking forays in the type and length of flights used to capture prey. Although the bird used the same mode of prey location (i.e., body pivoting and "Tail flashing", Section 12.4) in aerial feeding as in hawking forays, the flights were significantly longer (Table 35) and involved large amounts of acrobatic manoeuvres rather than direct flights.

TABLE 35. Lengths of "Hawking forays" and "Aerial feeding flights".

Mean length of "Hawking foray"	= 1.0 s
Range of lengths	= 0.5 - 2.5 s
Number of forays recorded	= 50
Mean length of "Aerial feeding flight"	= 7.0 s
Range	= 8.0 - 225 s
Number of flights recorded	= 44
$t = 7.4$, df = 92, $p > 0.01$, Appendix 7	

Aerial flights occurred in the canopy, above streams, and a large amount was seen in the Supra-littoral zone along the Kaikoura coast (April to

May 1975).

Because of a difficulty in obtaining cinematographic records on aerial feeding, a detailed description of the acrobatic manoeuvres used in prey capture could not be made.

9.3.2d "Ground feeding"

Ground feeding accounted for 17% of 1532 feeding observations and was the most common method employed in winter (Table 31).

The fantail often flew from a perch to land on the ground to stand with the tightly closed tail held 60° above the horizontal position. The tail fanned open when the bird "Waltzed" over twigs on the ground (Section 12.2.2) or before flights off the ground.

While the feet remained stationary on the ground, the body was pivoted through an arc of 180° and the rectrices flicked in and out. Although body pivoting did not always occur, the bird continuously moved its head from side-to-side.

After landing on the ground, the fantail performed one of the following activities:-

(i) hopped (with both feet raised at the same time) across the leaf litter, stopped and stood pivoting,

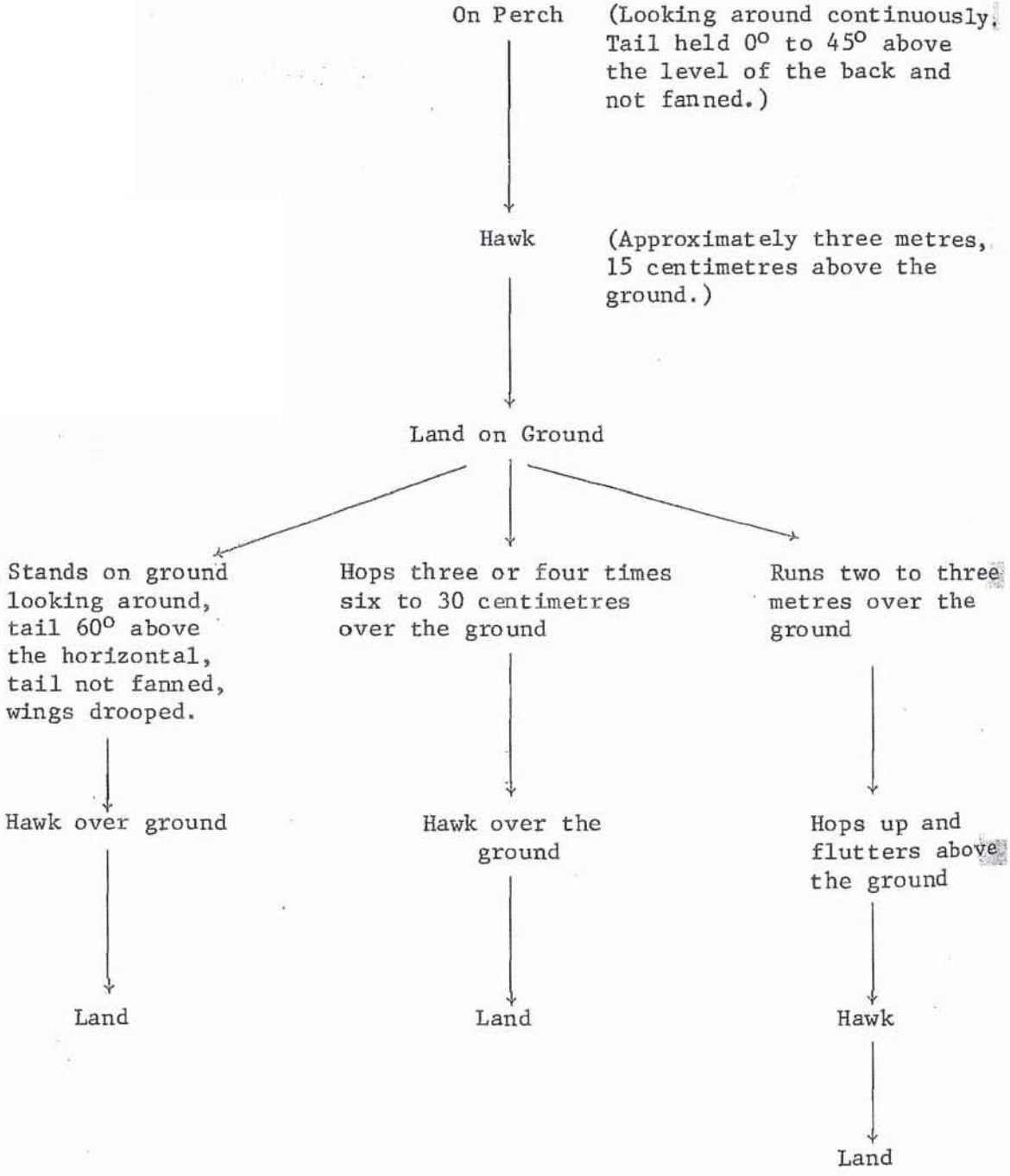
(ii) "Waltzed" over twigs on the ground, with the tail fanned and lowered to a position in line with the body,

(iii) jumped up, flew three to four metres (at a height of eight to 30 centimetres above the ground) and landed. This activity occurred in response to small insects flying above the ground,

(iv) flew one to two metres after hopping three or four times across the ground. The hopping appeared to disturb prey, or

(v) ran a distance of two to three metres, then hopped 30 to 90 centimetres above the ground, pirouetting and somersaulting in the air during each jump. Again this method appeared to disturb

Figure 13. Movements employed in "Ground feeding".



prey which were subsequently caught during acrobatic manoeuvres (Fig. 13).

There was a characteristic whipping up and down of the hindparts of the body and the tail (which was held 45° to 60° above the level of the back) as the bird ran over the ground. The whipping of the tail was probably the result of the running movements.

When standing, hopping or running on the ground the tail was rarely fanned and never lowered or dragged through the leaf litter. Very few observations of "Vertical tail flicking" (Section 12.3) were made and "Tail flashing" (Section 12.4) did not precede prey capture.

The South Island Fantail rarely probed the ground with its beak and I did not observe the bird using its feet to expose prey in the leaf litter.

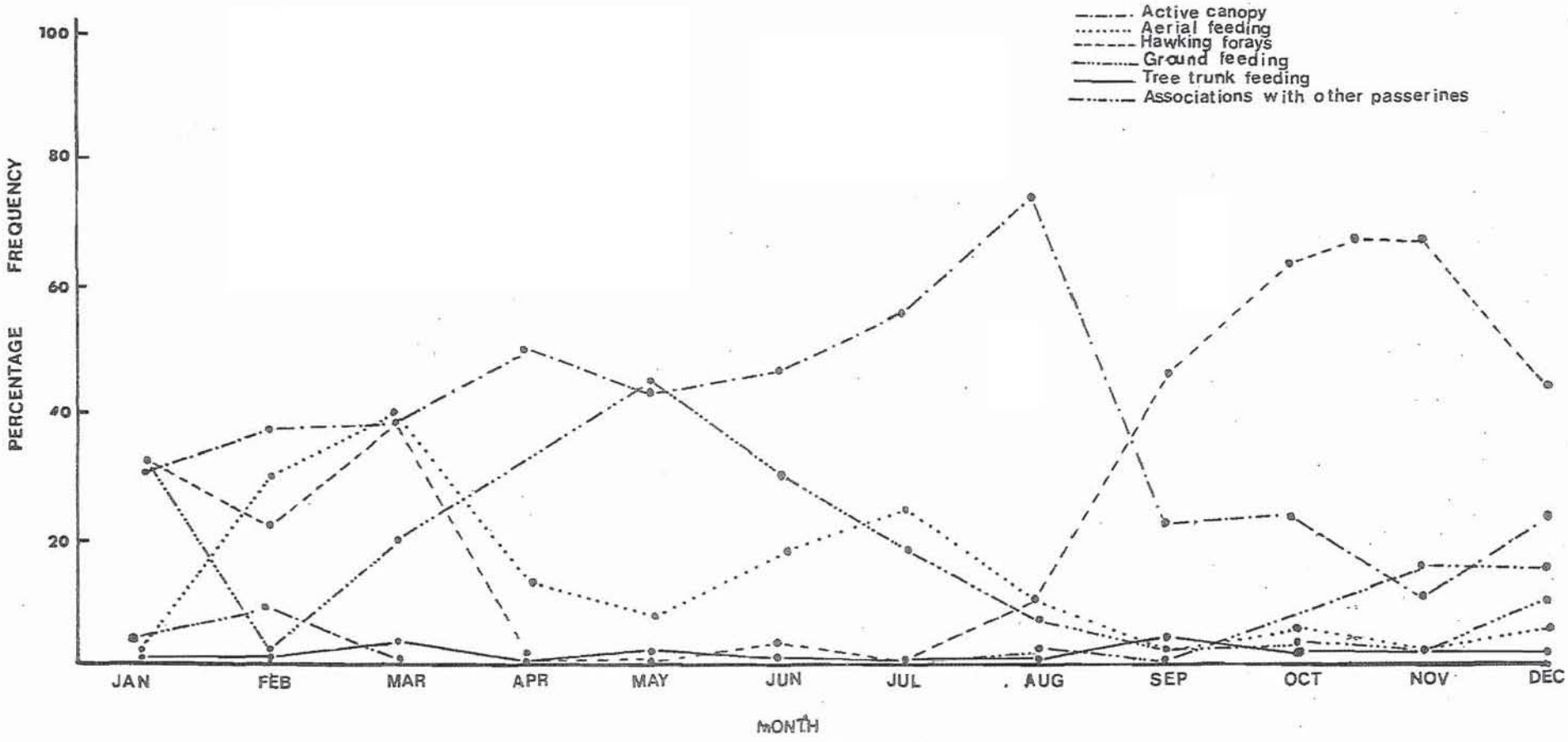
9.3.2e Feeding on Tree Trunks

Although "Tree-trunk feeding" only involved 6% of 1532 feeding observations 81 specific accounts of this method were recorded.

When the fantail clung to vertical tree trunks the tail was raised so that it lay 90° to the body and trunk surfaces. When the bird moved up, down or around the trunk, the fanned tail and wings were flicked (Section 12.3.2). After hopping up the trunk the fantail usually darted out from the surface and came back to the trunk to repeat the sequence. The bird rarely pecked at the trunk.

The fantail frequently clung for several seconds to the underside of horizontal limbs before swooping down to catch passing insects. When upside-down the tail and wings were fanned, the tail was in line with the body and the head was held at right angles to the long axis of the body in such a way that the bird was looking towards the ground.

FIGURE 14. Seasonal variation in prey capture.



9.3.3 Seasonal Variation in Prey Capture

The method of prey capture varied with season and weather conditions. In winter months the fantails spent most of their time on the ground and foraging through the lower and middlestorey. Compared with other modes of feeding, "Trunk feeding" was relatively infrequent, but more was seen in winter than at other times. For example, in May, 38 instances of fantails feeding from trunks were noted, 17% of the total feedings recorded. In contrast, no "Aerial feeding" and few instances of hawking for food were seen in that month. Fantails were often seen associating with silvereyes in winter (Table 36, Fig. 14).

As the breeding season commenced and the weather conditions improved there was a general trend of increasing aerial and hawking manoeuvres, and a decrease in feeding associations with silvereyes, "Active canopy feeding", ground and trunk feeding. This trend continued through August to November (Fig. 14).

By February breeding had ended and between February and April there was an increase in "Active canopy feeding" and "Ground feeding". Although there were large numbers of hawking and aerial feeding observations, the frequency had decreased markedly in comparison with that observed in the breeding season. The associations with silvereyes increased and may be due to a decrease in aggressiveness by the fantail (towards other species) as the breeding season ended (Section 11.3.1). The fantails also fed in association with each other at this stage. They often sat below and flew after prey stirred up by other fantails' movements through the foliage. Large numbers of moths resting on the underside of leaves were disturbed and subsequently caught in flight after the birds hopped or tumbled through the foliage. I did not observe the birds picking moths off the leaves, possibly because the moths were well camouflaged in the surrounding foliage.

TABLE 36. Seasonal variation in prey capture.

	Number of observations						Percentage frequency of observations					
	Active canopy	Aerial feeding	Hawking forays	Ground feeding	Tree-trunk feeding	In association with other passerines	Active canopy	Aerial feeding	Hawking forays	Ground feeding	Tree-trunk feeding	In association with other passerines
March	15	0	17	9	2	18	25	0	28	15	3	29
April	57	0	0	39	3	16	50	0	0	34	2	14
May	100	0	1	103	4	18	44	0	0	46	2	8
June	16	0	1	11	0	6	47	0	3	37	0	18
July	15	0	0	5	0	7	55	0	0	19	0	26
August	135	3	20	13	1	11	74	2	11	7	1	5
September	40	38	81	1	7	4	23	22	47	1	4	2
October	49	11	120	3	1	5	26	6	63	2	1	3
November	26	38	155	4	0	5	11	17	68	2	0	2
December	21	10	38	10	1	8	24	11	43	11	2	9
January	9	1	10	10	0	1	29	3	32	32	0	4
February	34	10	20	2	1	28	36	11	21	2	1	29

9.3.4 Prey Manipulation

Unlike small prey which were devoured during aerial flights, large active prey caught while hawking were usually subdued before they were swallowed. The prey was carried in the tip of the beak to a nearby branch. On a few occasions (9% of 80 observations) the prey was swallowed on alighting (Type 0). However, in most cases one of the following methods of subduing prey was used:-

(i) Type 1. The fantail twisted its body to one side, knocked the insect (which was held in the tip of the beak) on the branch once, returned to its forward position and swallowed the insect in a single gulp.

(ii) Type 2. The prey, held in the tip of the beak, was knocked once on each side of the fantail's body before the insect was devoured.

(iii) Type 3. The prey was knocked a large number of times on the branch. Occasionally I saw fantails tap their victims up to 50 times before swallowing them.

(iv) Type 4. The prey was transferred from the beak to the foot then clamped against the perch. After pecking, the insect was swallowed.

(v) Type 5. The prey was grasped by the foot which was positioned over the perch. Again the prey was pecked before it was swallowed.

(vi) Type 6. The foot holding the prey was placed under the perch during pecking.

(vii) Type 7. The prey was transferred to the foot, which clamped the insect to the perch. After the insect was pecked it was taken up by the beak, knocked on the perch and swallowed.

(viii) Type 8. Successive bouts of knocking and pecking of the prey

(which was clamped to the perch or grasped by the foot) occurred (Table 37).

TABLE 37. Methods of prey manipulation.

Method of prey manipulation	Number of observations	Percentage frequency of observations
Type 0	7	9
Type 1	7	9
Type 2	7	9
Type 3	12	15
Type 4	29	35
Type 5	7	9
Type 6	1	1
Type 7	6	8
Type 8	4	5
Total	80	100

There was little difference in the preference of subduing prey solely by knocking or pecking ($\chi^2 = 3.8$, df = 1, p = 0.05, Table 38). When the insect was placed in the foot the most frequent method of subduing was by clamping rather than grasping it away from the perch. The approach of the bill to the insect (held in the foot) was medial rather than lateral.

TABLE 38. Manipulation of the prey by knocking and pecking.

Method of manipulation	Number of observations	Percentage frequency of observations
Knocking only	26	41
Pecking only	37	59
Total	63	100

Less common observations of prey manipulation included: placing the prey on a wide branch, stepping on and over the insect before it was

picked up and swallowed; and the transfer of the prey (assisted by the beak) from one foot to another during a single observation.

When the prey was transferred from the beak to the foot, the bill was lowered as the foot was raised. At the same time the wing adjacent to the foot which grasps the insect was spread. Wing spreading functioned in maintaining balance but may secondarily assist recapture of prey, which was dropped frequently. In 19% of 77 observations the prey was temporarily lost. Loss and recapture (sometimes ten times during a single observation) was more frequent when large insects (e.g., blowflies) rather than small insects were taken to nestlings.

After the prey had been restrained the fantail attempted to swallow the insect by lifting and directing the head backwards as the beak was opened wide. On some occasions the insect was regurgitated and repeatedly knocked. The prey was always swallowed whole.

The eight methods of prey manipulation were observed under three circumstances:-

(a) before swallowing the prey,

(b) before the female was located and courtship fed, and

(c) before the prey was carried to the nestlings.

9.3.5 Feeding Associations between the South Island Fantail and other Small Passerines

The South Island Fantail was frequently observed feeding in association with other passerines. In Riccarton Bush, these associations were mainly restricted to the silvereyes although associations with Grey Warblers, Redpoll and Song Thrushes were recorded (Table 39).

The fantail was attracted to small groups of single silvereyes. Here it hawked out after food stirred up by the silvereyes' feeding tactics.

TABLE 39. Frequency of feeding associations with other passerines.

Species	Number of observations	Percentage frequency of observations
Silvereye	127	95
Grey Warbler	4	3
Redpoll	1	1
Song Thrush	1	1
Total	133	100

The fantail did actively seek out silvereyes but most associations appeared to be a result of a close proximity between the two species when feeding independently. If the birds were feeding in the same area the fantail immediately flew to a position near the silvereyes, where it sat 0.5 to 1.5 metres below the silvereyes, with tail fanned and wings spread. The fantail rarely sat above the silvereyes.

Before hawking to catch an insect, the tail was often flicked from a position in line with the back to one at right angles to the body. At the completion of a hawking foray, the fantail returned to its original perch or landed on the ground. From the ground the bird hopped up through the foliage or made a direct flight back to its original perch. Here it stood continuously watching the silvereyes for any object that dropped below them. On a number of occasions fantails chased leaves. However, they were not caught and sometimes the response of the fantail was merely to lunge forward. The lunge was accompanied with wing rotation which corrected the loss of balance and prevented falling.

Hawking was the main feeding method employed during the association, but a small amount of ground feeding below silvereye groups occurred.

Few vocalisations were given while feeding below the silvereyes. Soft "Contact type 1" calls, different from the loud "Type 1" calls given while foraging alone, were emitted occasionally. Although the fantails spent most of their time feeding below their associates they occasionally preened or rested with their tails closed.

Fantails followed the groups from branch to branch, tree to tree, and for distances of up to 900 metres, continuously hawking in the lower storey.

Most of the associations occurred in the non-breeding season (Section 11.3.1).

9.4 DISCUSSION

Very little information is available on any aspect of the feeding behaviour of the South Island Fantail. In this section I discuss the use of different feeding levels, seasonal variation in prey capture, methods of prey capture and commensal feeding by the fantail.

Many species of birds have a characteristic height preference for foraging activities. Diamond (1970) has recorded the height distribution for many New Guinea species of *Rhipidura*. However, there is very little information available on such preferences for the South Island Fantail. In this study there was little difference in the amount of feeding in the lower, middle and upperstoreys (Table 31). Although most foraging occurred on the branches, many observations of fantails feeding on the ground were made (Section 9.3.1). Stead (1932) stated that "Fantails do not often settle on the ground". However, I found that ground feeding was common, especially during the winter months when aerial prey was less abundant. Blowflies, moths and large swarms of flying insects frequently caught by the fantail during the summer months were not apparent in winter. As the breeding season commenced (at the

beginning of Spring - Section 3.3.6) the frequency of ground feeding decreased and feeding in the middle and upperstorey increased. These trends were probably due to the emergence of the larval stages of the aerial insects the fantail feeds on, and to the fact that the fantails were spending more time in the middle and upperstorey advertising their presence and territorial boundaries at this stage (Section 3.3.6). A similar trend of feeding on the ground and lowerstorey in the winter months and upperstorey during the warmer months "when larval and flying insect life was more abundant there" was observed by Blackburn (1967) when studying the Saddleback *Philesturnus caruncula tus*.

There were also seasonal changes in the methods of prey capture. In the warmer months when aerial prey was avilable the fantails caught insects on the wing during hawking forays and aerial feeding flights (Section 9.3.3). However, during the winter months the birds spent more time actively seeking out insects in the lower, middle and upperstorey (i.e., "Active canopy feeding"), feeding on the ground and in association with other passerines, particularly silvereyes (Table 36). These changes in methods of prey capture are probably due to the seasonal variation in types and abundance of prey.

Most of the New Guinea species of *Rhipidura* have been grouped into one of two foraging types. Firstly, those that actively seek out prey by moving through the middle spaces of the forest (Dimorphic Rufous Fantail *Rhipidura brachyrhyncha*, White-breasted Thicket Fantail *R. leucothorax clamosa*, and Black Fantail *R. dltra altra*) and secondly, those that perch on exposed branches waiting to catch any insect that passes by (Northern Fantail *R. rufiventris* and the Friendly Fantail *R. albolimbata* - Table 49). I suspect that there are a number of other common foraging methods employed by these species. The South Island Fantail used five distinct foraging methods, "Active canopy feeding",

"Hawking forays", "Aerial feeding", "Ground feeding" and "Tree-trunk feeding". In "Active canopy feeding" the fantails "Waltzed" along the branches and hopped from one branch to another. Although food was occasionally pecked from the branch surfaces, the movement through the branches was a means of increasing the area covered in which the prey could be located and caught during darts from the perch. The study of "Active canopy feeding" produced two important points with respect to "Tail fanning" and "Flicking" in the South Island Fantail. Firstly, "Tail fanning" occurred as the bird "Waltzed" along the branches, and "Vertical tail flicking" occurred before hopping from branch-to-branch (Sections 12.2.2 and 12.3.2). Secondly, the fantail used a very effective means of disturbing insects in the foliage, i.e. "Tumbling flights" (Section 9.3.2c).

Although "Hawking forays" are employed by many species of *Rhipidura* (Rand and Gilliard 1965) I have found no mention of "Aerial feeding". This could be due to differences in the types of prey in different habitats, or to a lack of distinction between the two methods by other researchers which is possible if detailed information on the nature and lengths of flights were not noted. The length of the fantail's tail, and ability to fan and close it quickly, probably makes "Aerial feeding" flights a very efficient method of prey capture.

The study of "Ground feeding" proved to be very important to this study for two reasons. Firstly, it was previously thought to be very uncommon (Stead 1932) and secondly because it provided some insight into the function of "Tail fanning" and "Flicking". "Ground feeding" used prey disturbance and subsequent hawking techniques. This disturbance resulted from the bird running over the ground, rather than "Tail-fanning", "Vertical tail flicking" or "Tail flashing (Sections 12.2, 12.3 and 12.4 for definitions). Fanning and flicking did not appear to

be related to "Ground feeding" which employed a different, successful means of disturbing prey (Section 9.3.2a).

Insectivorous birds often batter large or hard insects upon a branch before swallowing (Van Tyne and Berger 1966) and a number of passerines hold large insects against the perch with their feet while tearing them into smaller portions with the beak (Root 1967, Clark 1973). The South Island Fantail frequently knocked large insects upon branches before swallowing, and often held the prey against the perch with their feet (Table 38). However, instead of tearing the prey into smaller portions, the fantail merely pecked the prey (probably to subdue the insect) before swallowing it whole. Wakelin (1971) also noted a New Zealand Fantail holding a moth "parrot fashion", a method typical of the Fantail flycatchers (Parker 1967). When pecking the insect (held against the branch) the approach of the bill was medial rather than lateral. Medial approaches are typical of corvids, Corvidae, and titmice, Parvidae (Clark 1973). I believe the medial approach of a very sharp bill would be more effective in killing or subduing prey than the lateral approach.

An animal or bird moving about the bush may startle into activity other small insects or animals in which it has no interest. Consequently, a number of associations have evolved in which one species of animal or bird derives its food from that which another drives from hiding. There are many such associations among passerines, and there is reference to some species of *Rhipidura* associating with other birds (Deignan 1945). I frequently found fantails feeding in association with other passerines (Section 9.3.5), particularly silvereyes, during the winter months. There is probably no competition for food between the two species because of their different feeding niches. The silvereyes fed on:-

(i) food from bark surfaces and crevices, which were explored by the beak. The silvereye often hung or leaned over to investigate crevices on the underside of the branch,

(ii) food hidden in the foliage (particularly dried leaves) which were probed by the beak, and

(iii) clusters of berries, which the bird sometimes clung to and pecked. The silvereye often clung to the underside of the branch in an upside-down position.

The silvereye did not perform aerial attacks on prey, so food driven from hiding was available to any species capable of retrieving that which fell or flew below the foraging silvereyes. The close association between the fantail and silvereye, rather than other passerines, is probably due to the type of foraging activities employed by the silvereyes and the amount of prey that is disturbed. It is important to note that "Tail fanning" occurred when fantails were perched below the silvereyes (Section 12.2.2), a situation in which the fantail was not "Flushing" insects.

CHAPTER 10

CHAPTER 10

VOCALISATIONS OF THE SOUTH ISLAND FANTAIL

10.1 INTRODUCTION

Song is a vocal display in which one or more sounds are consistently repeated in a specific pattern. It is given mainly by males, usually during the brooding season. All other bird vocalisations are collectively termed call notes or simply calls which, in contrast to the songs, are brief sounds with a relatively simple acoustic structure.

Descriptions of the songs of various New Guinea species of *Rhipidura* have been made but these consist of brief phonetic interpretations (Diamond 1972). A detailed study on the vocalisations of the North Island Fantail has been undertaken

In this chapter a description and discussion of the South Island Fantail's vocalisations which include various calls; the male's song, the female's song and duetting, have been made. Notes on the behaviour associated with the vocalisations is given.

This chapter is not intended as a detailed study on the vocalisations of the fantail but merely supplements and provides more detailed information on terms (i.e., the names of the various vocalisation patterns) used in other sections of this thesis.

10.2 METHODS

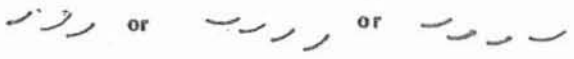
In any study on vocalisation patterns and behaviour, some method of recording song is essential. Many researchers use musical notations and phonetic interpretations which are of value primarily to their

FIGURE 15. Songs of the New Guinea fantails.

Rhipidura threnothorax

Rhipidura leucothorax

Rhipidura rufidorsa



Rhipidura brachyrhyncha

Rhipidura hyperythra

Rhipidura albolimbata

(a)  (b) (c)

Rhipidura rufiventris

Rhipidura leucophrys

(a) 

(b)

(c)

(from DIAMOND 1972)

authors. Diamond (1972) used such phonetic interpretations when studying the songs of many New Guinea species of *Rhipidura* (Fig. 15). Recently, with the development of sound spectrograms, songs can be analysed in more detail and with much greater precision. In the production of sonograms sounds are magnetically recorded on a metal disc and then transmitted through various modulations and oscillators to a stylus which automatically writes on a cylindrical drum. The drum is synchronised with the revolutions of a recorder disc. The stylus, electrically activated, leaves a series of lines. Higher and lower tones are shown on a vertical axis, time or rhythm on a horizontal axis and amplitude or loudness of the song by the depth of shading. For more detailed information on sound spectrograms and their analysis see Collias and Joos (1953), Kellogg and Stein (1953), Kellogg (1960), Thorpe (1961) and Greenewelt (1968).

The equipment used to record bird songs must have a high quality and fidelity and respond uniformly to a wide range of sound frequencies in cycles per second if spectrographic analysis is required. Such equipment usually involves expensive magnetic tape recorders, large parabolic reflectors and directional microphones. These were not readily available during this study and, because I did not intend making a detailed study of song structure but merely provide the reader with some indication of the general composition of the fantail's vocalisation, I did not use any sophisiticated recording equipment. Vocalisations were recorded on a Philips EL3302 portable cassette recorder which had a frequency range of 80-10,000 Hz. I attempted to reduce the effect extraneous sounds by attaching the microphone, which was partially enclosed in a foam casing, on a long pole. The microphone was directed at the fantail, often as close as 60 centimetres.

Although sound spectrographs have considerable advantages over

the phonetic interpretations unless the reader has made a study of the method and analysis of spectrographs, sonagrams may provide little information. For this reason I have included a cassette tape of some of the vocalisations of the South Island Fantail with this thesis.

Information on the time between calls and vocalisation were obtained from tape-recordings. Individual variation and number of phrases in specific songs were recognised by ear within three months of the start of fieldwork. Consequently, a study on differences in the length of songs between individuals and at different stages of the breeding season could be made.

A study on diurnal and seasonal variation in song was made. This began in April 1975 and ended in November 1975. Although I would have liked to have made a 12 month study on this aspect, the time involved would have resulted in a less detailed study of the breeding behaviour. By choosing these months to study seasonal variation in song I obtained information on changes in the frequency in singing as winter commenced, during winter, and as the breeding season began at the start of summer (Section 3.3.6). The study of seasonal variation in song was undertaken at a private property in Christchurch. The property was in a residential area (Cashmere Hills), but because it was located on a hill the songs carried long distances and a study of approximately 12 birds was made. Each week, one morning (from 0700h to 1200h) and one afternoon (from 1200h to 1900h) study was made. At the end of each half hour I recorded the number of calls and songs heard during each half hour period. The figures only give a rough indication of the seasonal variation of song frequency and cannot be used for detailed month by month comparisons because of the effects of population changes. It is probable, however, that population changes were small.

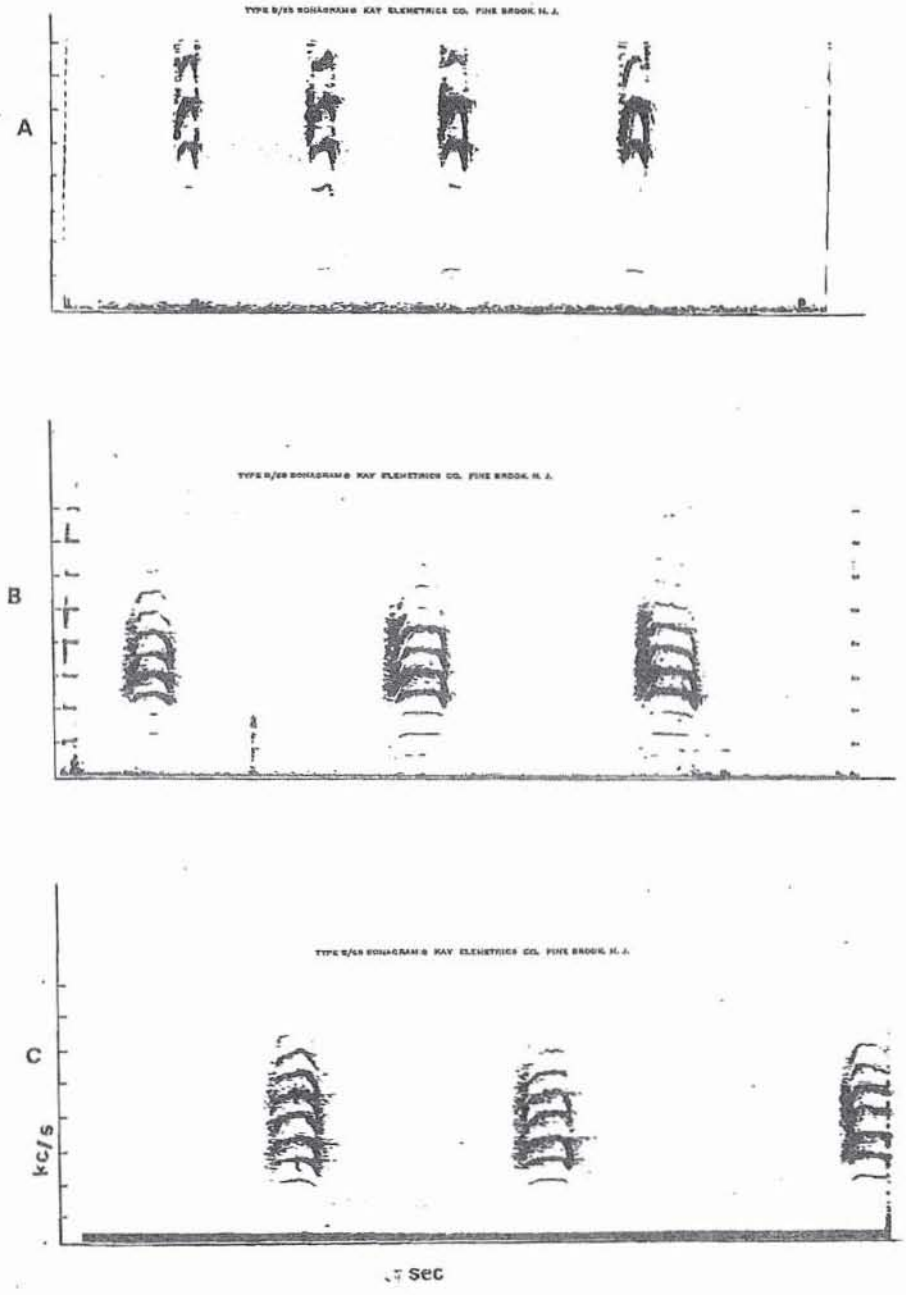

A
B
C
kc/s
sec

PLATE 2. "Type 1" calls of the South Island Fantail.

A. Sonagram of the call using a narrow filter.

B. Sonagram of the call using a wide filter to obtain more information on the number of harmonics above 8 Kc/s.

C. Sonagram from a different recording of "Type 1" calling.

10.3 RESULTS

10.3.1 Calls

Five calls were identified and named "Type 1", "Contact type 1", "Fast type 1", "Type 2" and the "Feeding vocalisation".

10.3.1a "Type 1" calls

"Type 1" calls consist of notes of approximately 0.1 second in length with a fundamental at five kc/s and three harmonics at 7.5, 8.0 and 8.5 kc/s respectively. The notes are uttered in succession with periods of approximately 0.4 seconds between notes (Plate 2; cassette tape, Track 1, part A).

"Type 1" calls were often given as the fantails foraged, preened, collected nest material, and while flying towards the nest to build or relieve an incubating or brooding mate. Although the fantails gave an average of two calls per seven second interval while foraging and collecting nest material (Table 40), the rate increased to an average of seven calls per seven second interval during flights towards the nest. The increase in the rate of calling did not usually occur until the bird was within eight metres of the nest.

The call was given by both sexes throughout the year. However, there was a decrease in the amount of calling in the winter months (Fig. 16). There appeared to be a mid-morning and mid-afternoon peak in the frequency of calling, with a noticeable decrease before nightfall and at dawn (Fig. 17).

"Type 1" calls were given by solitary birds and were not always given in response to calls or vocalisations of other fantails.

10.3.1b "Contact type 1" calls

This call resembled "Type 1" in structure but was slightly harsher and only audible over short distances. The call, which was only heard in the breeding season, was visually given in the nest-site when

FIGURE 16. Seasonal changes in the amount of "Type 1" calling.

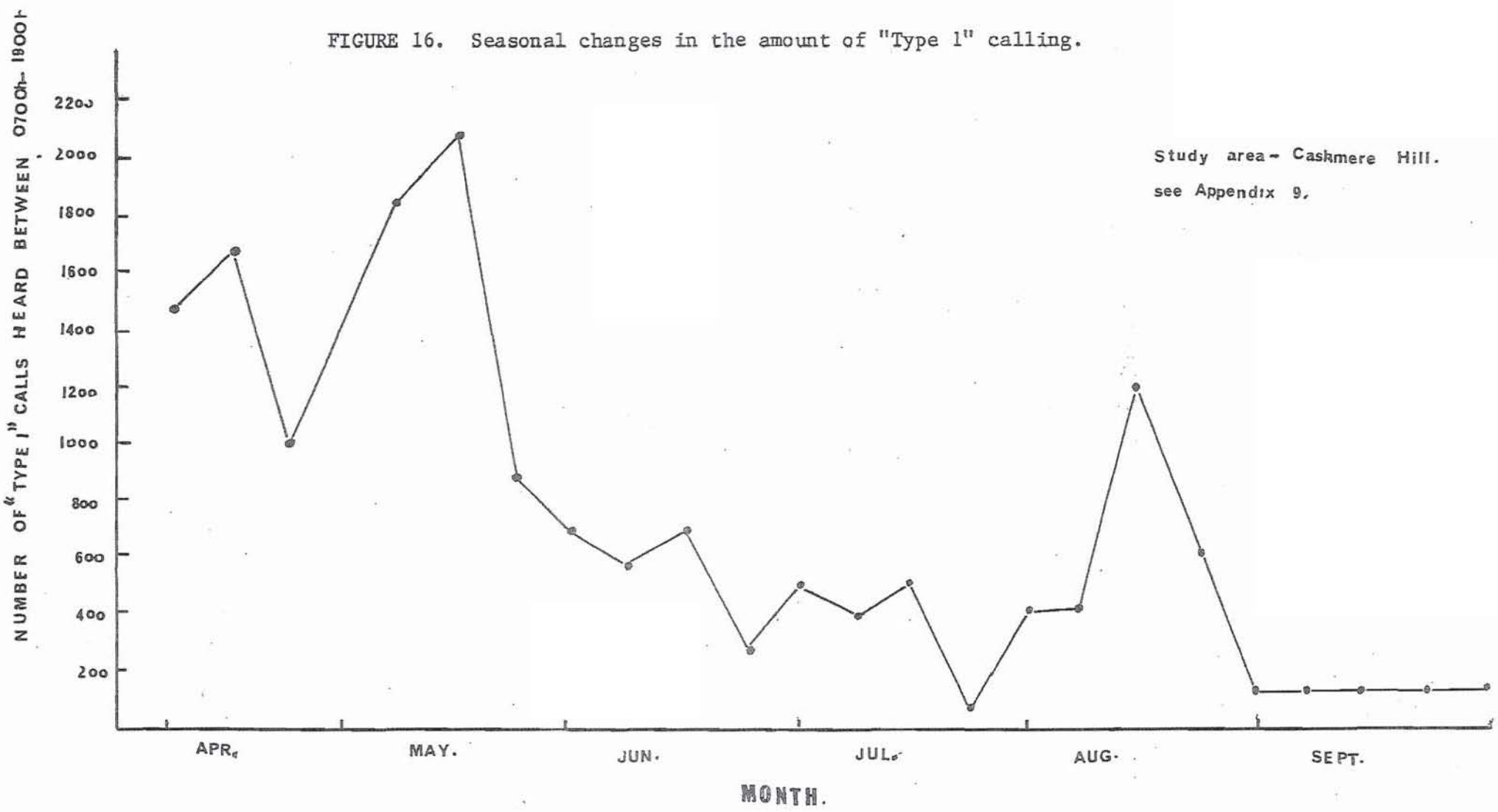
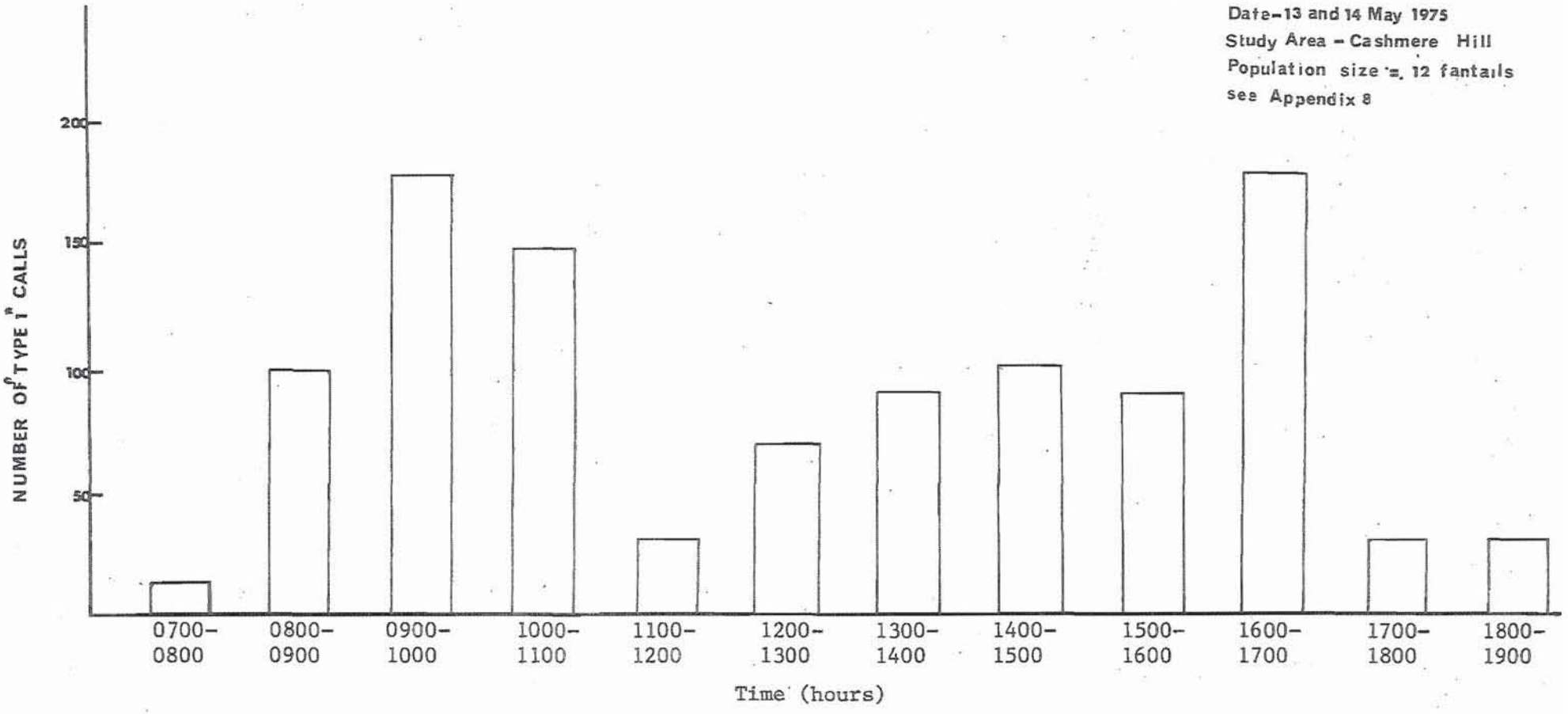
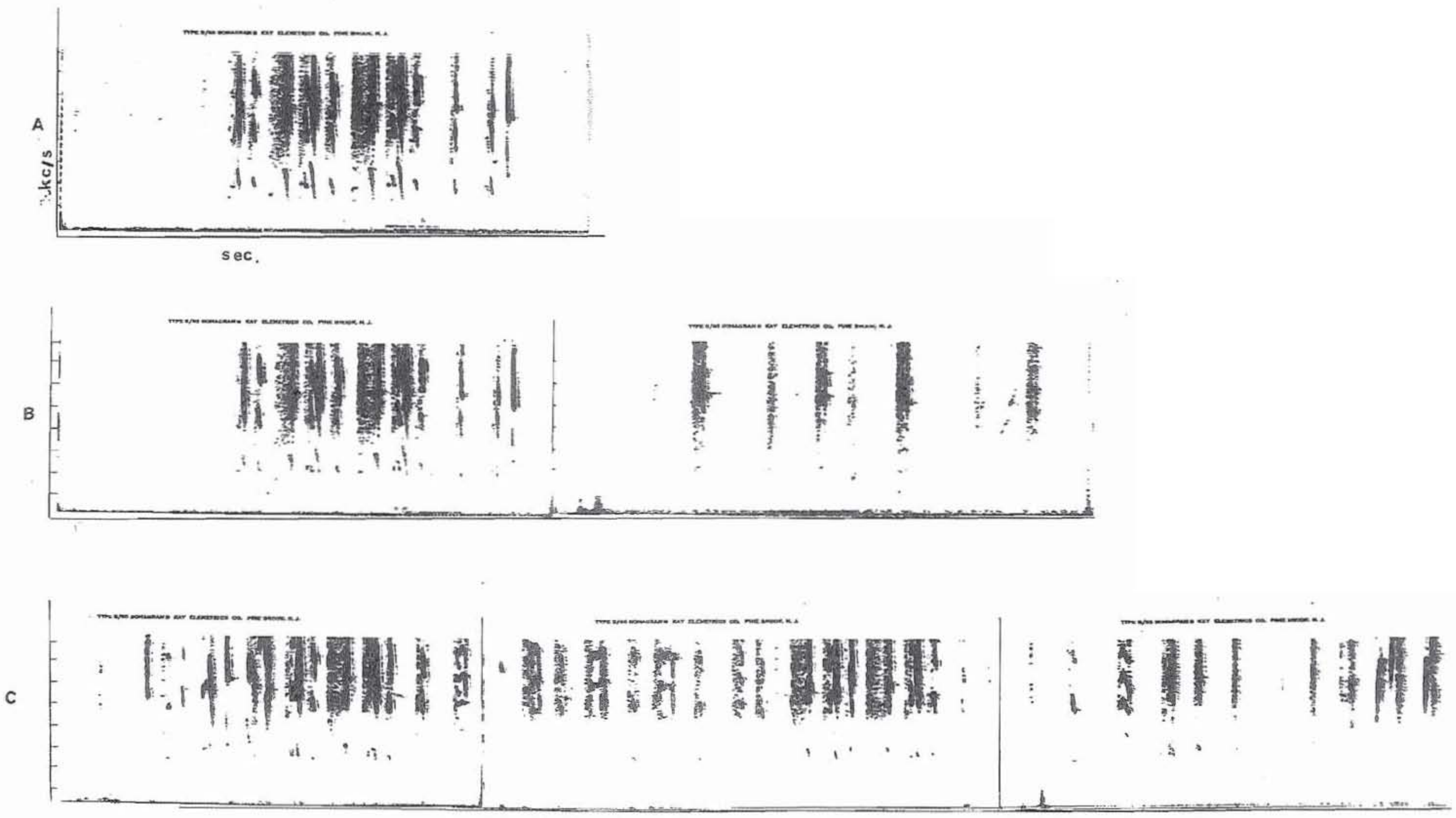


FIGURE 17. Diurnal variation in the frequency of "Type 1" calling.





A
kc/s
sec.
B
C

PLATE 3. "Type 2" calls of the South Island Fantail.

the fantails were collecting nest-material. This call was given by both sexes who called alternately when within two metres of each other.

10.3.1c "Fast type 1" calls

This call also resembled "Type 1" calls except that they were often louder and emitted at a significantly faster rate of 14 calls per 15 second interval (Table 40).

TABLE 40. Number of "Type 1" and "Fast type 1" calls given per seven second interval.

	Number of "Type 1" calls/seven sec.	Number "Fast type 1" calls/seven sec.
Mean	2	14
Range	20	17
Sample size	0-5	11-17
T = 4.7, df = 35, p > 0.01 - Appendix 6.		

These calls were given by both sexes throughout the year under a number of circumstances which included:-

(i) chases between fantails. The "Fast type 1" call was given in flight when one fantail was chasing or attacking another,

(ii) mobbing responses (Section 11.3),

(iii) bathing (Section 8.3.1b).

The call was occasionally given by the female when the male approached and was particularly evident when I tried to catch an injured fantail.

"Fast type 1" calls often preceded "Type 2" and "Type 3" calls and a short phrase of approximately five notes was often given in the middle of the "Type 2" vocalisation.

10.3.1d "Type 2" calls

Unlike the previous calls which consisted of a single note or a repetition of the same notes, this call incorporated a number of different notes. The fantail utters more than one note at a time at

FIGURE 18. Seasonal changes in the amount of "Type 2" calling.

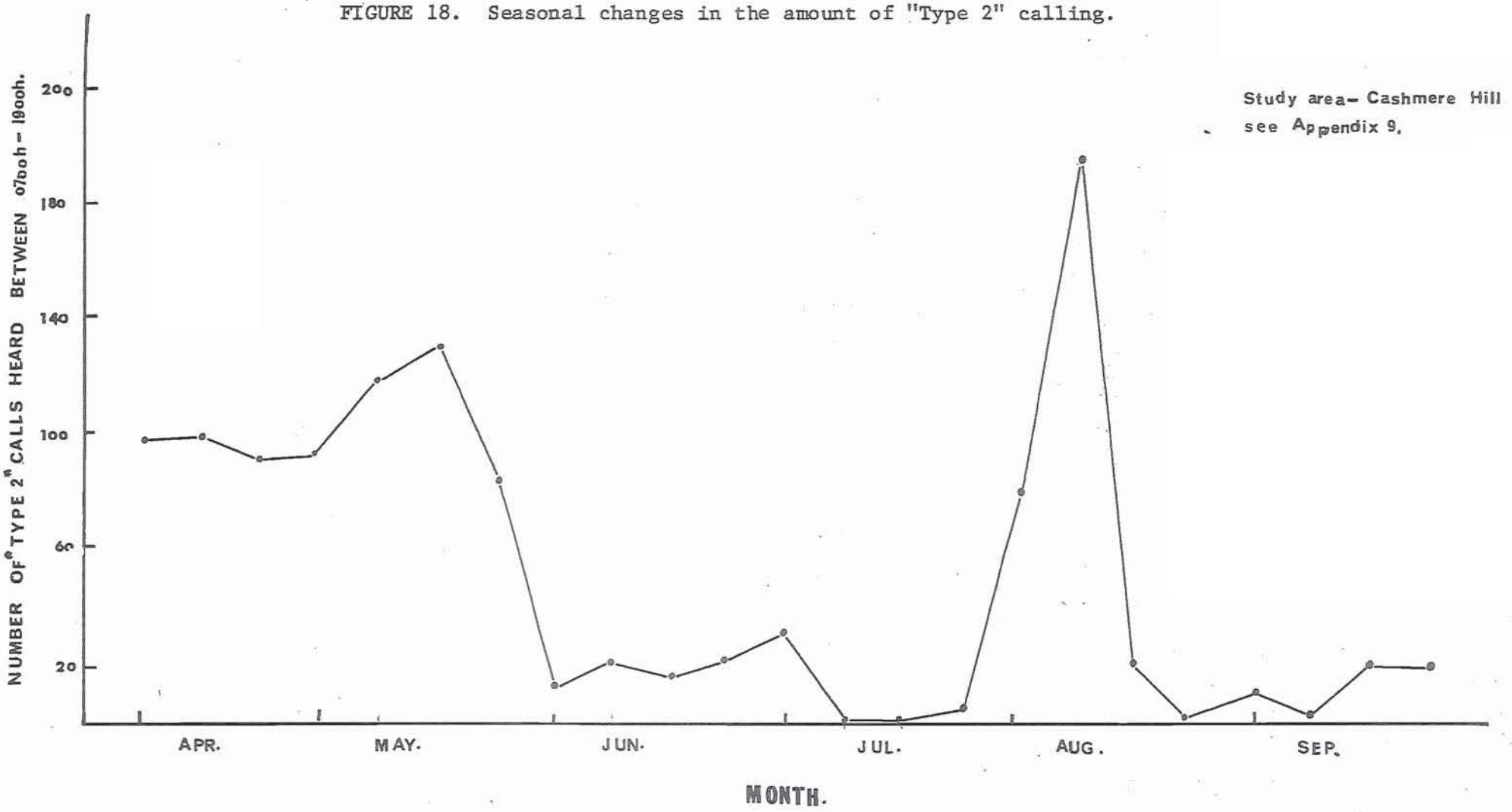
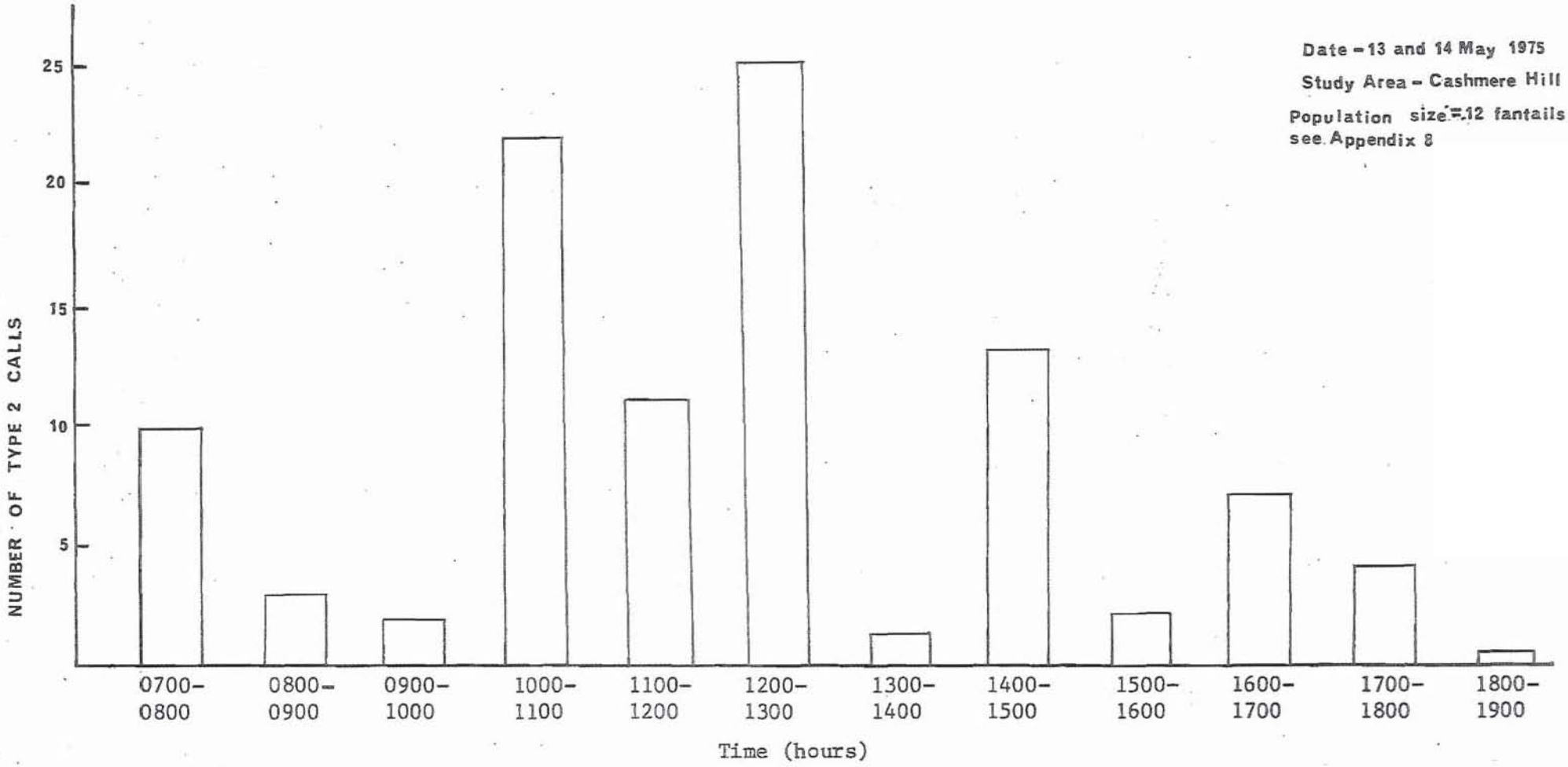


FIGURE 19. Diurnal variation in the frequency of "Type 2" calling.



different pitches, in quick succession. The frequency range of the notes extends from one to eight kc/s, and periods as short as 0.05 to 0.2 seconds between notes occur. Occasionally a "Type 1" note in between phrases of the "Type 2" calls is given (Plate 3; Cassette tape, track 1, Part B.

"Type 2" calls characterised chases and attacks on neighbouring fantails. The call was occasionally given while foraging, after hawking forays, while feeding fledglings, and when disturbed by the Ranger or myself. "Type 2" calls, given by the female, usually attracted the male who approached and either chased, sang or gave the "Wing-shivering" display.

Although the call was mainly given when fantails were together, it was also given by solitary birds.

The call was given at all the feeding levels as the bird stood on one spot, pivoting from side-to-side. Although the call was given throughout the year it occurred less frequently in the winter months (Fig. 18). There was a sudden increase in the number of "Type 2" calls at the beginning of the breeding season (August) when territorial boundaries were being established. There was no significant diurnal variation in the number of "Type 2" calls given (Fig. 19).

10.3.1e "Feeding vocalisation"

This call consisted of a series of two note phrases. The first note of the phrase was of a higher frequency than the second. Both notes resembled the "Type 1" call. This vocalisation was only given under two circumstances. These were:-

(i) while the female and male pivoted on the nest-rim before feeding nestlings, and

(ii) when the male "tried" to find the female to "Courtship feed" her. The male occasionally appeared near the nest and gave the vocalisation while holding an insect in the beak.

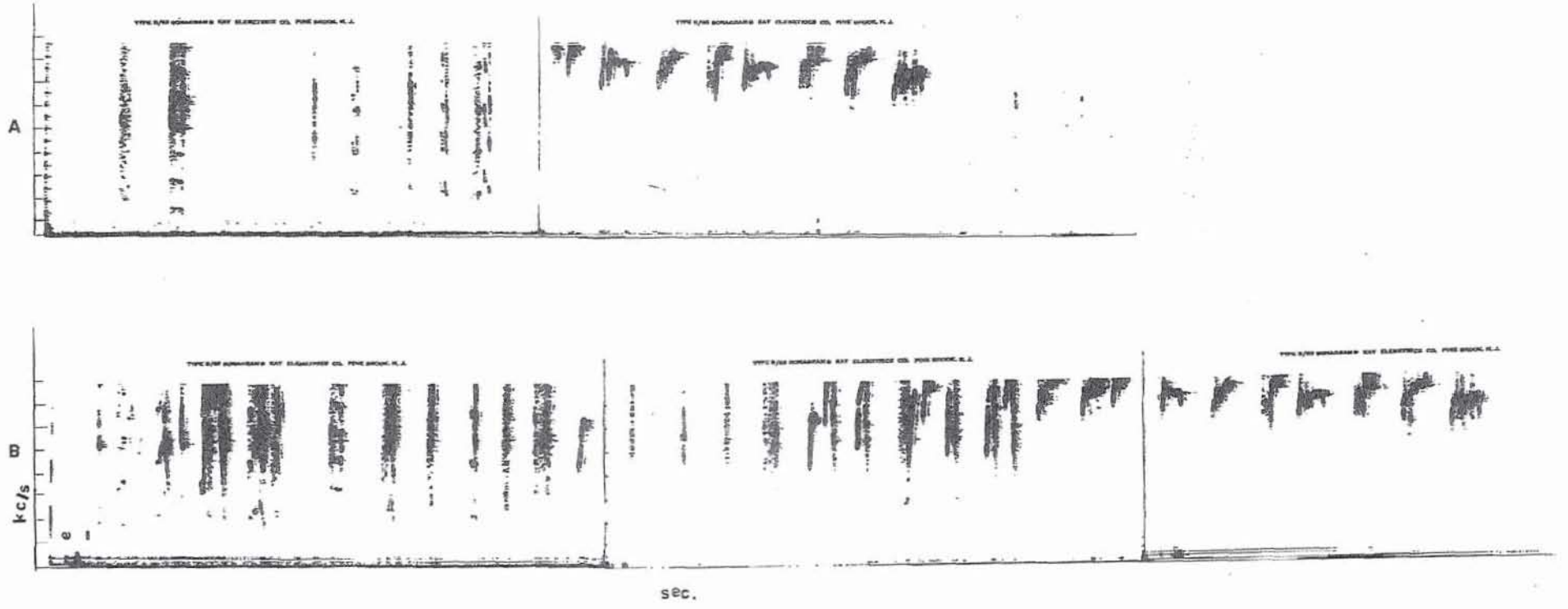

A
B
kc/s
sec.

PLATE 4. The song of the male South Island Fantail.

If the female responsed by calling, the male flew to her and fed her, but if there was no response by the female the male continued calling for several seconds then swallowed the prey. The call was only heard in the breeding season.

10.3.2 Male Song "Type 3" Vocalisation

The song of the male fantail consisted of two parts: the trill, which comprised the introductory series of notes uttered in quick succession; and the terminal part. The frequency range of the trill, which lasted from 0.5 to 1.5 seconds, was very wide, i.e., from one to eight kc/sec (Plate 4; Cassette tape, track 2). The terminal part of the song was composed of a number of three note phrases which had a frequency range of six to ten kc/s. The last part of each did not vary in pitch as much as the first part. The first two notes of the phrase were at a slightly higher pitch (the trailing part of the note being at about 6.5 kc/s) than the third, which had the trailing pitch of six kc/s. The notes in the terminal part of the song were approximately 0.2 seconds in length and as many as 12 were uttered within 3.1 seconds. Each three note phrase was repeated, sometimes only once but occasionally 12 to 19 times, producing songs 0.6 to 11 seconds long. However, most songs consisted of three, four or five phrases. There was no apparent difference in the number of phrases given by different fantails (Table 41).

There was no change in the length of songs during the breeding season. In P2R the male's song during September, October and November usually consisted of three to five phrases (Table 42). This trend was also apparent in the songs of P2B (Table 42).

The song was given in all parts of the bush, sometimes on the ground but usually on exposed perches. At the beginning of the breeding season the birds tended to sing more frequently in the canopy than in

TABLE 41. Variations in the length of songs given by different males.

Pair	Month	Occurrence: Trill	Occurrence: Number of phrases in each song 1	2	3	4	5	6	7	8	9	10	11	Occurrence: Tot.	Percentage frequency of occurrence: Trill	Percentage frequency of occurrence: Number of phrases in each song 1	2	3	4	5	6	7	8	9	10	11	Tot.
P1R	Oct.	100	61	62	156	219	155	85	45	19	10	6	6	924	11	7	7	17	24	17*	9	5	2	1	0	0	100
	Nov.	23	16	17	29	57	62	34	24	5	17	10	9	303	8	5	6	10	19	21	11	8	2	4	3	3	100
P2R	Oct.	8	23	9	25	38	40	36	40	17	15	2	0	253	3	9	4	10	15	16	14	16	7	6	1	0	100
	Nov.	8	9	5	28	30	20	18	20	1	4	2	0	145	6	6	3	19	21	14	12	14	1	3	1	0	100
P2B	Oct.	19	16	20	26	28	16	12	16	7	1	0	2	163	12	10	12	16	17	10	7	10	4	1	0	1	100
	Nov.	112	192	177	205	108	63	43	27	7	2	4	1	941	12	20	19	22	11	7	5	3	1	0	0	0	100

* The most frequently given songs by each pair are underlined.

TABLE 42. The length of the P2R male's song during the breeding season.

Observations recorded during the weeks dated	Occurrence													Percentage frequency of occurrence										
		Number of phrases in each song													Number of phrases in each song										
	trill	1	2	3	4	5	6	7	8	9	10	11	Tot.	trill	1	2	3	4	5	6	7	8	9	10	11	Tot.
11/9/75 - 18/9/75	9	13	21	47	62	50	53	42	23	11	8	1	340	3	4	6	14	18	15	16	12*	7	3	2	0	100
19/9/75 - 16/9/75	14	6	19	3	30	49	66	47	45	29	19	5	332	4	2	6	14	14	19	14	13	8	6	2	0	100
27/9/75 - 4/10/75	37	43	34	78	114	117	93	68	46	28	6	0	664	6	6	5	12	17	18	14	10	7	4	1	0	100
5/10/75 - 12/10/75	8	23	9	25	38	40	36	40	17	15	2	0	253	3	9	4	10	15	16	14	16	7	6	1	0	100
13/10/75 - 20/10/75	3	2	2	10	19	28	11	15	9	6	1	0	106	3	2	2	9	18	26	10	14	8	6	1	0	100
21/10/75 - 28/10/75	5	16	12	38	38	38	24	17	3	2	0	0	193	3	8	6	20	20	20	12	9	2	1	0	0	100
29/10/75 - 4/11/75	7	3	3	14	16	8	3	6	0	0	0	0	60	12	5	5	23	27	13	5	10	0	0	0	0	100
5/11/75 - 12/11/75	8	9	5	28	30	20	18	20	1	4	2	0	145	6	6	3	19	21	14	12	14	1	3	1	0	100
13/11/75 - 20/11/75	23	21	7	40	56	50	35	27	14	5	4	0	282	8	7	2	14	20	18	12	10	5	2	1	0	283
21/11/75 - 28/11/75																										

* The most frequently given songs for each week are underlines.

FIGURE 20. Diurnal variation in the frequency of singing.

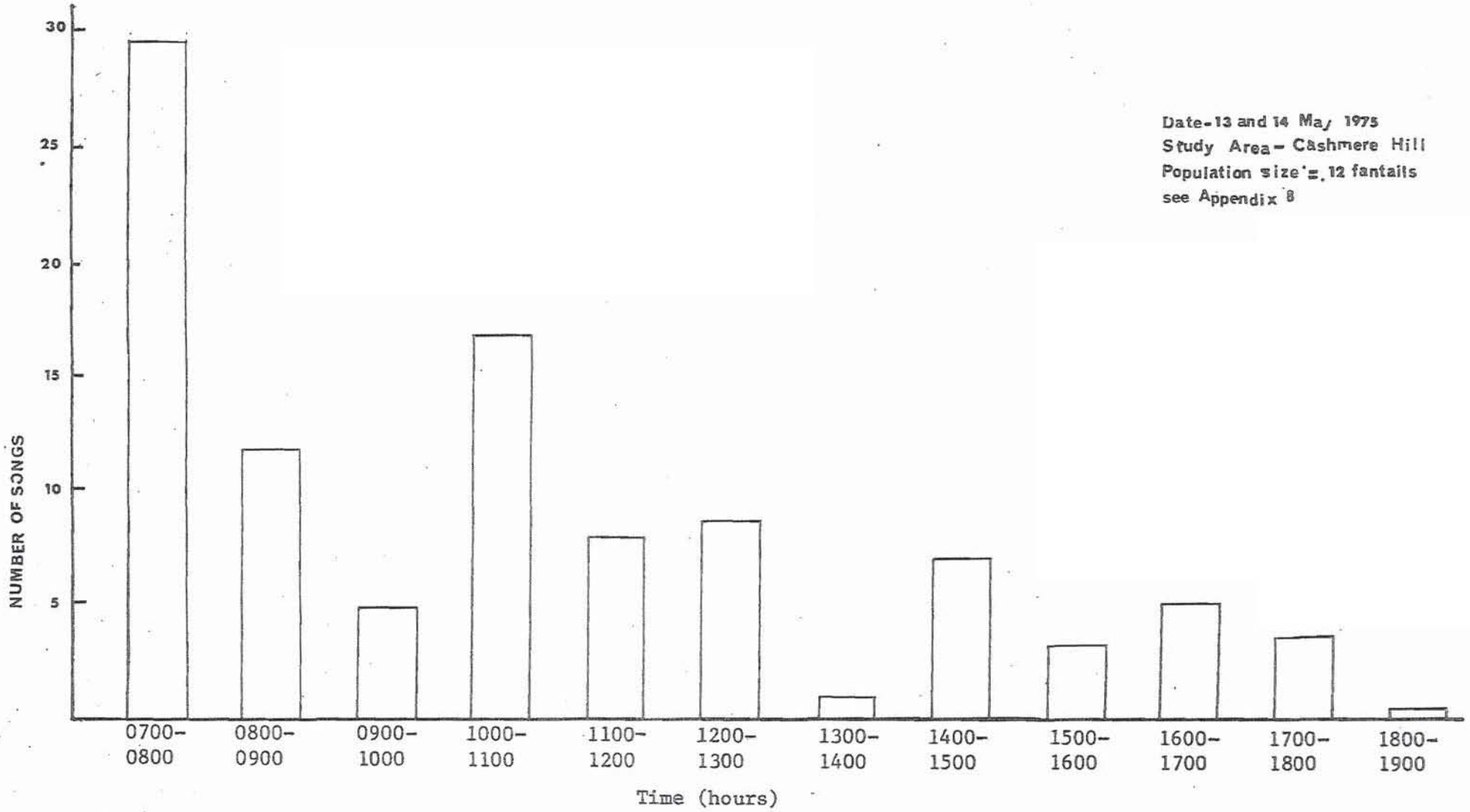


FIGURE 21. Seasonal change in the amount of singing by the male.

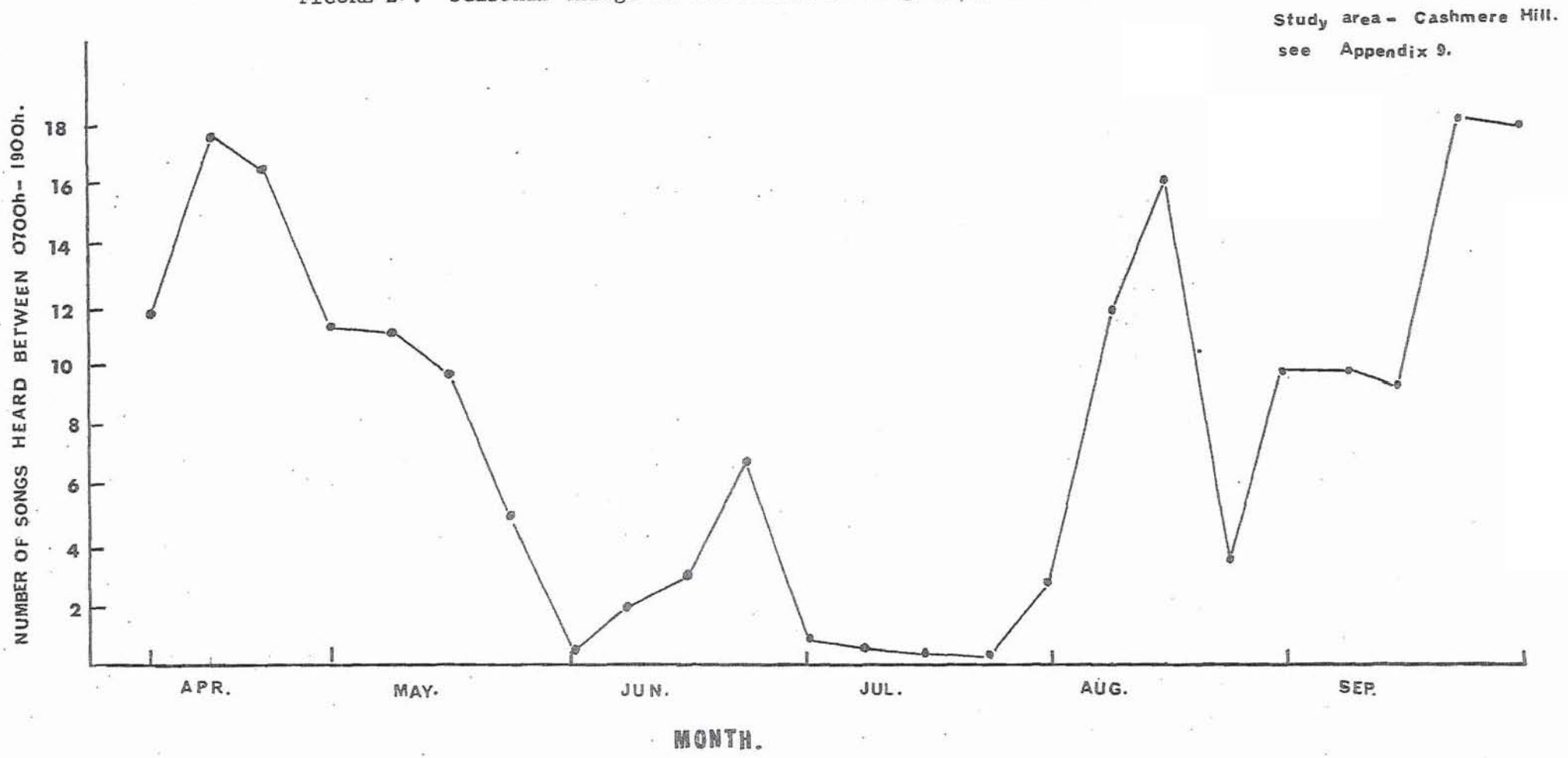


FIGURE 22. Changes in the amount of "Dawn singing" as winter commences.

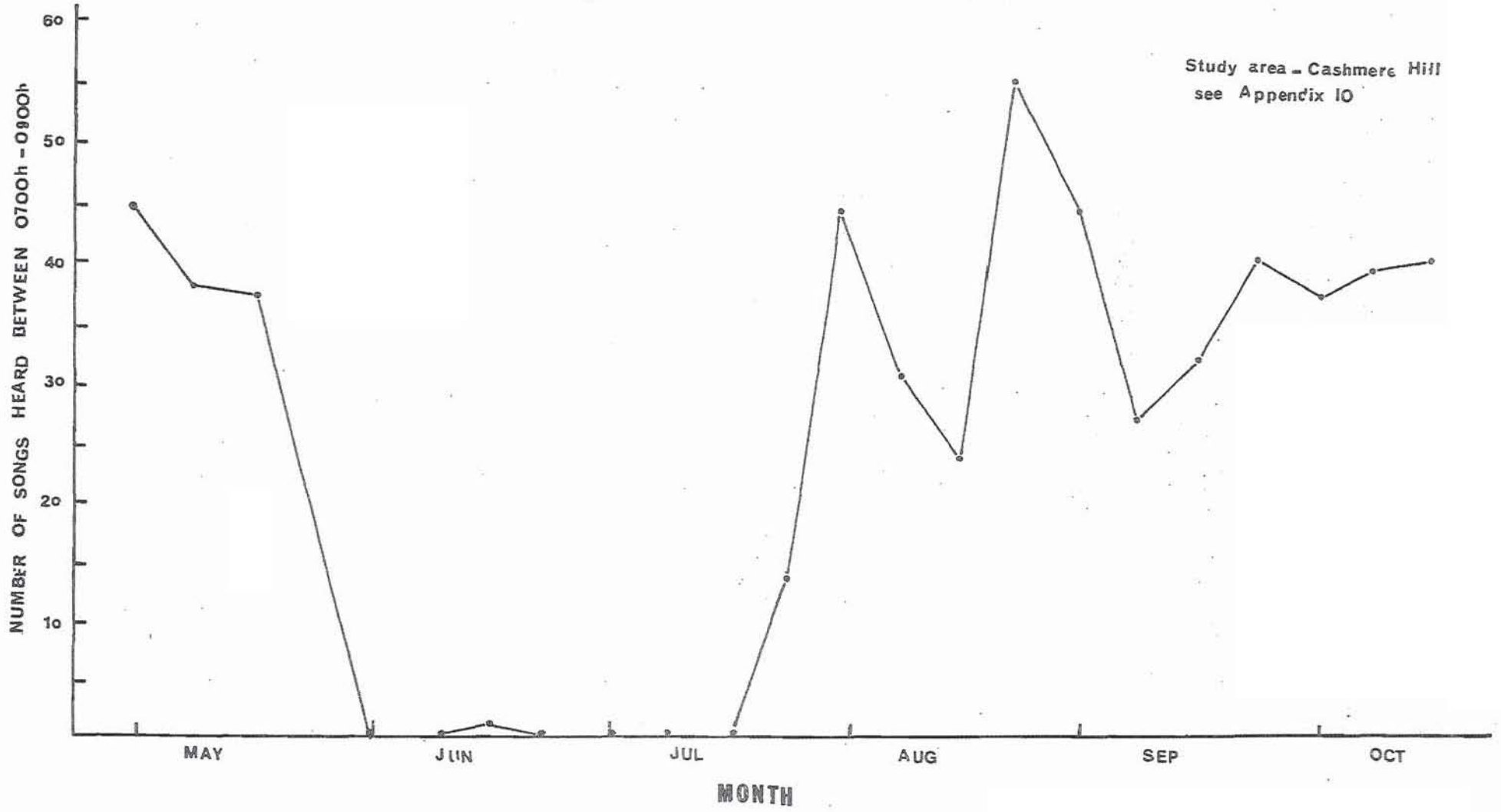
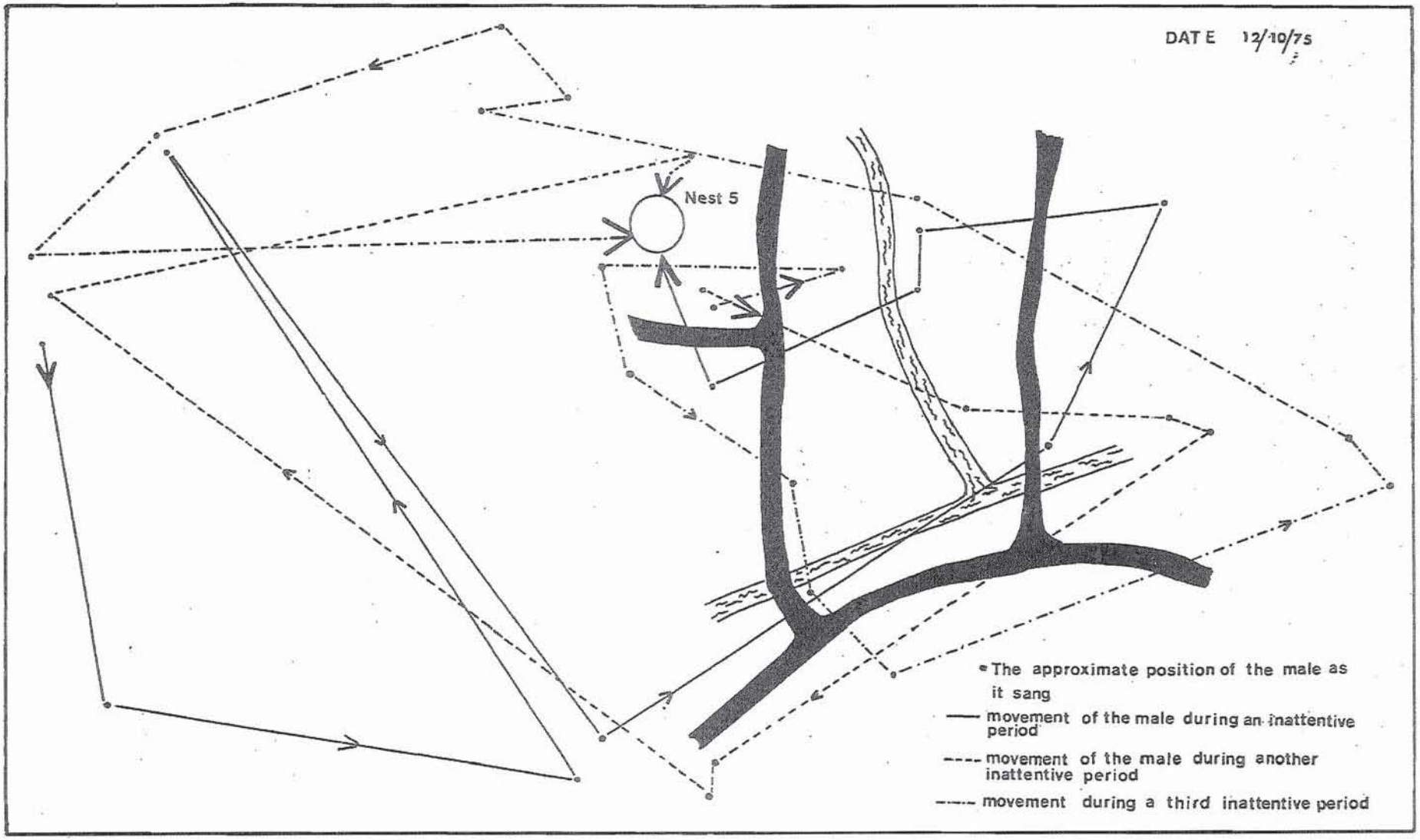


FIGURE 23. Singing along territorial boundaries during inattentive periods in the incubation period.



the other foraging levels, i.e., the lower, middle and upperstoreys.

There was some diurnal variation in the frequency of singing. As the sun rose, the fantail continuously sang for about 30 minutes and then slightly less frequently for the next two hours. There was an even greater decrease in the number of songs given after 0900h (Fig. 20). This trend was apparent during the summer months, but as winter approached there was an abrupt cessation in dawn singing and a general decline in the number of songs sung each day (Fig. 21, Fig. 22).

The song was given throughout the year, in the winter months and at all stages in the breeding season. As the female built the nest the male often sang nearby and occasionally flew around the territory singing at regular intervals. Once incubation began, a regularity in male singing was even more evident. After the female relieved the male, he sang near the nest then flew around the territorial boundaries (Fig. 23) singing at regular intervals until he returned to relieve his mate. He continued to sing during the nestling and fledgling stage but less frequently and with less regularity.

Song was given under a number of circumstances besides those mentioned above (i.e., when setting up breeding territories and when advertising territorial boundaries). The male sang:-

(i) after leaving the nest and waiting for the female to return to incubate,

(ii) after threatening me,

(iii) while foraging, and

(iv) when perched.

Counter-singing, which involved the alternate singing of one male with a neighbouring male some distance away, was apparent.

10.3.3 Female Song

The female rarely sang and although the general structure of the

TABLE 43. Variations in the length of the female's song.

	Occurrence													Percentage frequency of occurrence										
		Number of phrases in each song													Number of phrases in each song										
Pair	trill	1	2	3	4	5	6	7	8	9	10	11	Total	trill	1	2	3	4	5	6	7	8	9	10	11	Total
P1R	5	17	4	3	2	0	0	0	0	0	0	0	31	15	55	14*	10	6	0	0	0	0	0	0	0	100
P2R	73	19	73	60	23	6	0	0	1	0	0	0	427	17	45	17	14	5	1	0	0	0	0	0	0	100
P1B	14	30	11	6	11	1	0	0	0	0	0	0	73	20	41	15	8	15	1	0	0	0	0	0	0	100
P2B	5	16	6	11	8	4	3	0	0	0	0	0	53	9	30	11	21	18	7	6	0	0	0	0	0	100

* The most frequently given song by the female of each pair is underlined.

song resembled that of the male's, the song was weaker, less rhythmic and consisted of much fewer phrases. The female frequently gave songs consisting of the trill part only, or the trill and one phrase. Although the male gave songs with as many as 19 phrases in, the longest song heard by the female consisted of eight phrases (Table 43).

The female occasionally sang during the nest-building stage and after leaving the nest during the incubation and brooding periods. The male responded to the female's song in a number of ways. He usually approached her and gave "Type 2" vocalisations or song. He occasionally chased her, copulated or followed her.

10.3.4 Duetting

In the breeding season the male and female occasionally sang in unison, i.e., both sang identical phrases at the same time. In 50% of 14 duets both birds started singing at the same time. The fantails did not usually finish singing at the same time; one often gave an additional one or two phrases.

On all the occasions when duetting was noted the fantails were in close visual contact, one to two metres away from each other.

10.4 DISCUSSION

In this study call-notes were concerned with the coordination of the behaviour of other members of the species, mostly in situations which were not primarily sexual but rather concerned with such maintenance activities as feeding, territorial defense, and communication of distressing or alarming situations.

"Fast type 1" calls were given when fantails were distressed, particularly during the mobbing response (Section 11.3) and probably functioned in putting other fantails in the area on alert or attracting them to the area to join in the mobbing response.

"Type 2" calls were associated with most chases and threats towards intruding fantails, and occasionally towards the female. The call appeared to communicate threat and probably assists territorial defense. The "Feeding vocalisation" had two functions. Firstly, when given on the nest rim the call stimulated gaping in the young. A similar vocalisation was noted by Hough (1969) when studying the Willie Wagtail. Secondly, it signalled the male's readiness to "Courtship feed". The call was aimed to attract the female but more importantly, to strengthen the pair-bond as a result of the act of "Courtship feeding". The function of the most frequently given call, i.e., "Type 1" calls, is not so clear. This call was given throughout the year, by solitary birds in the winter months, by pair members in the breeding season, and groups of fantails in the post-breeding season. The call was not restricted to any specific situation. The only suggestion I can make as to its function is that it is a response to mild distress situations. This is based on two facts. Firstly, the call was similar to the distress call but was given at a slower rate, and secondly because the call was often stimulated by excessive noise as I moved through the bush.

The songs of most passerines tend to be associated with territorial defense, establishment and maintenance of pair bonds and the coordination of the activities of birds, particularly of a mated pair. The song of the male fantail plays all these roles. The fact that the fantail establishes winter feeding territories accounts for the presence of song in the winter months when it functions in advertising territorial boundaries and probably serves as a substitute for physical combat. The sharp increase in the number of songs given at the beginning of the breeding season clearly points to its role as a means of signalling the male's presence and territorial boundaries, and attracting females.

Once the pair-bond is established, singing ceases in many passerine species, particularly during the nestling stage (Thorpe 1961). This was not the case with the fantail who continued singing throughout the nest-building, egg-laying, incubation and brooding stages of the breeding season. Although the length of the songs did not change with each stage (Table 42) the frequency of calling did. The rate of calling remained fairly constant during the nest-building, egg-laying and incubation stages but there appeared to be a decrease in the number of calls given during the nestling and fledgling periods, probably because the demands on the male by the young for food were too great to allow time to advertise and frequently defend territorial boundaries. The differences in presence or absence of song after pair-bond formation between the fantail and other passerines are probably due to differences in the general breeding behaviour of the species. In the fantail the female does most of the nest-building, leaving the male free to sing along territorial boundaries. He can continue singing during the incubation period because the female shares the role of incubation equally with the male. Singing probably ceases after pair-formation in those species where the male builds the nest, incubates or feeds the female while she incubates; situations which prevent singing because of the time employed in other activities.

"As a rule, species do not sing near their nests. When males approach their nests for one purpose or another, they are inclined to be silent or to sing much more softly" (Pettingill 1970). The fact that the fantail frequently sings near the nest suggests that the concealment of the nest is not essential in this species and that the fantail's predators probably rely on visual rather than auditory cues.

A few species of passerines sing more or less continuously all day but the fantail, like a large proportion of diurnal species, sings more

frequently in the early morning. The fact that singing did not always occur at exactly the same time each morning can be explained by the fact that the amount of light rather than the time of day determines the beginning of singing in the morning and of singing in the evening. The abrupt cessation of early morning singing in May (Fig. 22) may be the result of changes in weather condition, particularly heavy frosts which may inhibit singing.

In recent years research on duetting, in which the female sings simultaneously and on a par with her mate, has attracted much attention. Duetting has been recorded in a number of passerines in Central and South America, Africa, and more recently New Guinea and South-West Pacific (Diamond and Terborgh 1968, Diamond 1972a). Although Diamond (1972a) noted the presence of duetting in nine species of passerines throughout the South-West Pacific no mention was made of its presence in any species of *Rhipidura*. This study confirms the fact that the South Island Fantail engages in "Unison duetting", in which the male and female sing virtually identical phrases in unison. The fact that the pair did not always start singing, or end, at exactly the same time may be due to lack of experience. Studies on captive birds have made it clear that a pair of birds learn to duet in perfect synchrony only after many months of practice (Diamond and Terborgh 1965). The role of duetting is still far from clear. Thorpe (1961) believes that duetting and antiphonal singing may serve to maintain the sex-partnership where the territorial function of song is reduced or absent. Diamond and Terborgh (1968) have suggested that duetting may fill "the need" for birds living in dense vegetation where visual contact is difficult to evolve intricate vocal displays rather than visual displays. Because the fantail's song plays an important role in the defense of territorial boundaries, and the fact that in most cases the fantails were often

in immediate visual contact, the interpretation that duetting birds favour the development of vocal rather than visual displays because they live in dense thickets does not apply in the fantail. I believe that duetting functions in strengthening the pair-bond by ensuring recognition of members of the pair. While duetting, one bird, probably, the female, learns the other's song. The learning of his song may ultimately lead to a better recognition of him rather than other birds which have slightly different songs. Very little work has been done on this aspect. It would be interesting to know whether the female learns the male's song or vice versa. A study of the female's and male's song at the beginning of the breeding season (i.e., before duetting has occurred to any great extent) and at the end of the breeding season may provide some insight into the changes in song which may result from the practice obtained while duetting.

CHAPTER 11

CHAPTER 11

INTER-SPECIFIC INTERACTIONS

11.1 INTRODUCTION

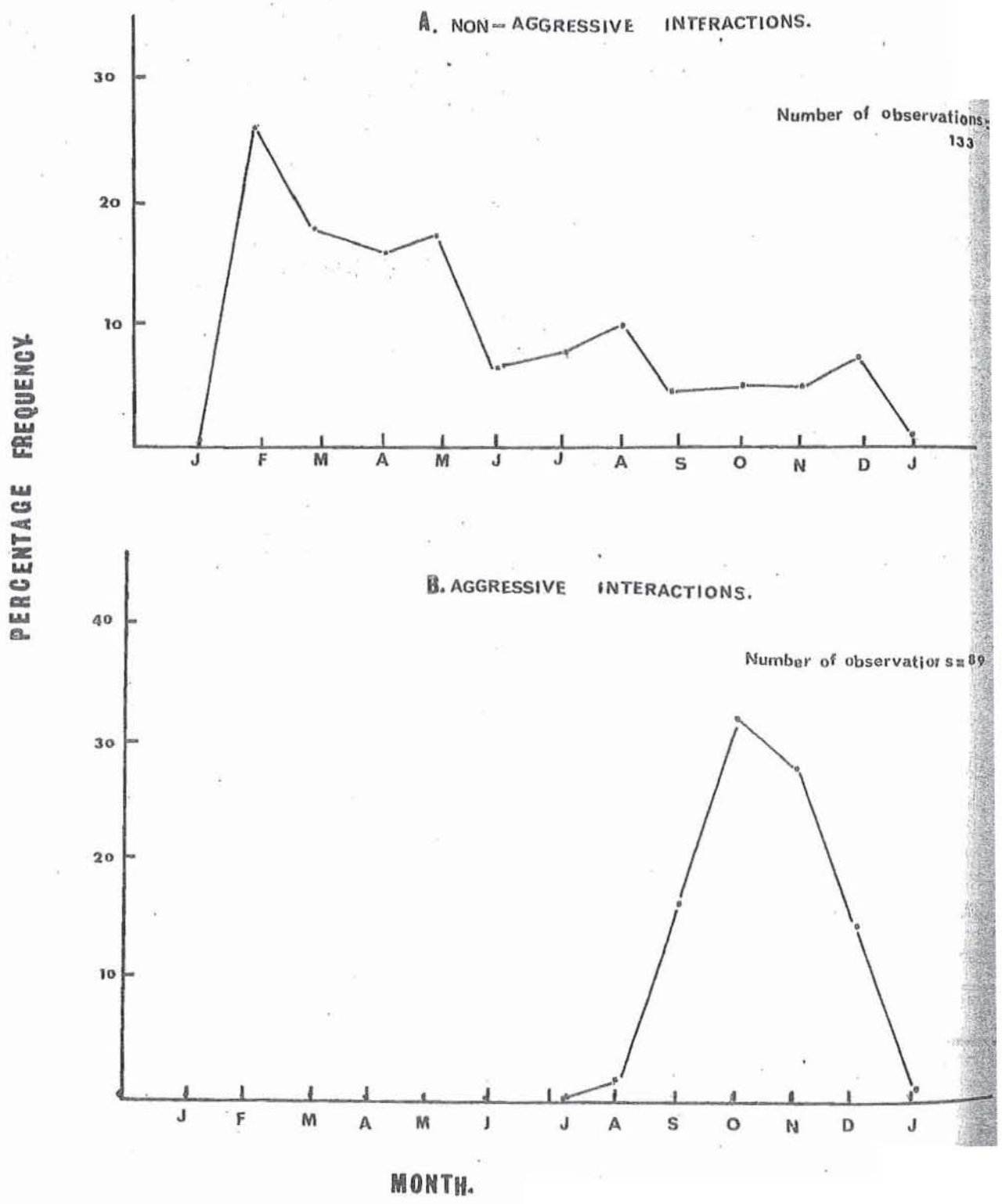
Like many other researchers and naturalists, Oliver (1955) describes the interaction between the fantail and Man in the following way:- "The Pied Fantail is common in all parts of the country and quickly makes its presence known, coming right up to the visitor. So fearless and friendly is it that it will remain in the vicinity and even settle upon him between its numerous short excursions into the air to catch insects". I question the South Island Fantail's "friendliness" after noting the fantail's behaviour around me, other passerines and potential predators. A description and discussion of this behaviour form the basis for this chapter.

This chapter also describes mobbing behaviour defined by Hartley (1938) as "a demonstration made by a bird against a potential or supposed enemy belonging to another and more powerful species, and is not a reaction to an attack upon the person, mate, nest, eggs and young". Hinde (1954) and Altmann (1956) have recorded detailed descriptions of mobbing behaviour in a number of passerines, but I could not find a record of it in any species of *Rhipidura*. Because of my inadequate number of observations, this study can only indicate the presence of a mobbing response in the fantail.

11.2 METHODS

A description of the fantail's behaviour and the presence of

FIGURE 24. Interactions between fantails and other passerines.



"Tail fanning", "Vertical flicking" and "Tail flashing" was noted during interactions between the fantail and other passerines, cats, a hedgehog and a New Zealand Falcon, *Falco novaeseelandiae*. Notes on the response of the fantail to myself were made.

11.3 RESULTS

11.3.1 Interactions with other Passerines

In this study interactions between passerines were:-

(i) non-aggressive. These accounted for all the interactions during the non-breeding season (February to March), including the feeding relationship between the fantail and silvereye (Section 9.3.5). A small number of non-aggressive interactions occurred during the breeding season (Fig. 24), and

(ii) aggressive. Seventy-three per cent of 89 interactions in the breeding season (August to January) were of this type.

As the breeding season commenced, the number of non-aggressive interactions between silvereyes and fantails decreased and aggressive encounters increased (Fig. 24). The first attack on the thrush was observed at this stage. This passerine was the most frequently attacked species (57%, n = 89). Other birds attacked during the breeding season included: the Blackbird, Chaffinch, House Sparrow and Grey Warbler (Table 44). Most of these species were perched when they were attacked.

Attacks and subsequent chases, resulted from a close proximity of the intruder to the nest during nest-building, incubation and breeding, or to parents feeding fledglings. This stimulated one of a number of responses (depending on the circumstances) which included:-

(i) an attack by the female, when the male was absent. This accounted for 27% of 79 observations (Table 45). The attack usually interrupted her nest-building, incubation or brooding behaviour,

TABLE 44. Species of passerines attacked by the fantail.

Species	Number of observations	Percentage frequency of observations
Song Thrush	52	58
Silvereye	24	27
Blackbird	8	9
Chaffinch	3	3
House Sparrow	2	2
Grey Warbler	1	1
Total	89	100

TABLE 45. The participation of the sexes in attacks on passerines.

Sex of the fantail attacking the passerine	Number of observations	Percentage frequency of observations
Female only	21	27
Female, assisted by male	11	14
Male only	34	43
Male, assisted by female	3	3
Simultaneous attack by female and male	10	13
Total	79	100

(ii) an initial attack by the female, who was subsequently aided by the male. In 14% of the observations the male approached or flew out of the nest on hearing "Fast type 1" calls or pecking (sounds characteristic of an attack).

(iii) an attack by the male only was the most frequent response (43%).

(iv) an initial attack by the male, who was later assisted by the female, occurred in 4% of the observations. The female usually deserted the nest to help her mate, and

(v) a simultaneous attack by both birds occurred in 13% of the observations.

These results indicate a larger degree of aggressiveness in the male than the female. The male tended to attack more frequently when he was alone.

A single bird attacked a passerine on the ground by diving within six centimetres of its head, or "fluttered" around the intruder. The attack was accompanied by pecking (directed at the head or back), a "Throat rattle", and "Fast type 1" calls (which were given during flights towards the bird and on alighting. The bird being attacked usually stood motionless (with beak gaped), or continuously turned to face its attacker. Attacks on perched birds were similar.

When both fantails attacked, they flew across the intruder simultaneously. As one fantail flew towards the bird, fluttering above and pecking at the head, the other fantail flew from behind, pecking at the bird's back. This tactic appeared to 'confuse' the intruder who continuously turned in an attempt to defend itself.

The length of attacks varied from 15 seconds to 12 minutes and usually ended with the male in close pursuit of the intruder as the female returned to the nest or sat preening. The male returned to the nest-site after the chase and subsequently sang, preened or entered the

nest. "Wing-shivering" (Section 4.3.4a) by the fantail, after an attack, occurred in only 4% of the observations.

11.3.2 Attacks on the Observer and New Zealand Pigeon

Unlike the more aggressive attacks on thrushes and silvereyes, approaches towards me (and less frequently, i.e. ten times, to the New Zealand Pigeon) were of a more agonistic nature, i.e., they incorporated approach and retreat tendencies rather than overt aggressive components.

The fantail approached me in one of the following ways:-

(i) hopped from branch to branch around me at a radius of two to six metres. In between hops the fantail stood facing me and pivoted,

(ii) flew as close as five centimetres, then swerved away,

(iii) approached, hovered in mid-air approximately one metre from me, then returned to the original perch,

(iv) hovered over my head before flying away, or

(v) "dived" over my head, causing me to "duck" down.

Less aggressive encounters, which occurred during experimental work with tape-recorders and flash-bulbs, were characterised by approaches, close scrutiny, displacement preening, "Yawning", mandibulatory movements or movements towards and away from me.

Mobbing behaviour was directed towards me when I attempted to catch an injured fantail. Two fantails appeared as the distressed bird gave "Fast type 1" calls while fluttering over the ground and up on to a perch. The other fantails sat close by, pivoting and occasionally calling "Type 1" before flying off.

11.3.3 Interactions with Cats, Dogs and a Hedgehog

The response of fantails to dogs was observed five times.

Dogs produced little response; except close scrutiny, pivoting, side-flicking of outer rectrices, and occasional "Type 1" calls. Mobbing behaviour was triggered by the presence of a cat on five occasions and a hedgehog once. In this study, fantail mobbing behaviour was characterised by "Fast type 1" calls and attraction of conspecifics (often as many as eight) who sat on perches within a two metre radius of each other. The birds sat approximately two metres from the cat and one and a half metres above the ground with wings slightly raised, tail closed, but rectirces flicked out as the body pivoted. The birds occasionally hopped from perch-to-perch but flights towards and over the cat did not occur. When one of the cats leaped up at a fantail there was a sudden burst of "Type 1" calls. Four of the five cat-fantail interactions incorporated mobbing behaviour and occurred at the end of the breeding season when large numbers of juveniles were observed in the bush. A less intense interaction occurred during the winter months.

11.3.4 Two Interactions between Fantails and the New Zealand Falcon

A live, tethered New Zealand Falcon was taken into Riccarton Bush, but did not produce a high intensity mobbing response, i.e., the attraction of a large number of fantails. Nick Fox tied the falcon to a fallen log before we quietly moved four to six metres away to stand in the bush. Within three minutes, three fantails appeared. Very few vocalisations were given by the falcon, so the fantails were probably attracted by the noise the falcon made while fluttering about on the log, or by visual cues. The fantails spent most of the time perched, pivoting, approaching, fluttering above the falcon and returning to the perches of nearby trees. On a number of occasions one bird landed on the ground 1.5 metres from the falcon. It stood pivoting but did not call until the falcon lunged forward. The fantail responded by jumping

up and giving a series of loud "Type 1" calls as it flew to a nearby perch. No other fantails were attracted to the area by the movement of the falcon or behaviour of the fantails.

A similar response was given at a second station in the bush. Only two fantails approached the falcon. The first spent most of its time feeding, and the second gave a large amount of "Type 2" vocalisations as it chased the first away.

The response by the fantail to the falcon in this study differed from that reported by Porter and Dawson (1968). They noted North Island Fantails, along with many other passerines, taking to the trees and giving alarm calls when a falcon flew by. The differences in responses may be attributed to differences between natural and experimental conditions.

11.4 DISCUSSION

The frequency of aggressive approaches, accompanied by vocalisations ("Type 2" and "Fast type 1") otherwise confined to aggressive situations, suggests that the belief of the "Friendly Fantail" is false and probably resulted from observations made by researchers with little knowledge of the bird's general behaviour and vocalisations. These observers seem to have confused curiosity, which results in approaches of the fantail to people in the bush, with friendliness, an anthropomorphic term we tend to relate with the beauty of the fantail form. This behavioural study cannot confirm the belief and goes further to suggest that the fantail, although very curious, is a very aggressive bird both to conspecifics and individuals of other bird and animal species.

Smythies (1960) and Goodwin (1967) describe the Pied Fantail Flycatcher and Willie Wagtail respectively as being aggressive birds.

The Willie Wagtail has been seen to attack and drive away large birds, such as Wedge-tailed Eagles, brown hawks, laughing Kookaburras and Magpies (Frith 1976). The South Island Fantail appeared to be particularly aggressive towards the thrush (Table 44). It is difficult to determine the cause of the higher frequency of attacks on this species because negative responses (i.e., a lack of a response) to all passerines in the nest-site were not recorded. Therefore the higher frequency of attacks on the thrush could be due to a higher frequency of observations for that species. However, it could also be due to the fact that the thrush usually ran over the ground below the nest in much the same way as a predatory rodent or mammal would. The fantail may not be responding specifically to the thrush but to the movement of an object over the ground near the nest.

The low intensity response to the New Zealand Falcon (a potentially dangerous predator) could have been due to the fact that it was tethered to a log, rather than in flight. It is very difficult to draw any conclusions about the response of the fantail to the falcon from this study because the falcon was taken into the bush only once.

I suspect that a mobbing response by the fantail to predators does exist. A further study on this aspect is warranted and a study on the response of the fantail to various models and stuffed owls, falcons and mustelids could prove interesting.

"Tail fanning", "Vertical tail flicking" and "Tail flashing" were not particularly evident during the interactions between the fantail and other passerines, myself, cats, and the New Zealand Falcon. Fanning and flicking did occur, but no more so than when the fantail was by itself. Fanning and flicking appeared to be related to the movements of the fantail rather than the mobbing response.

CHAPTER 12

PLATE 5. "Tail fanning".

PLATE 6. The fantail with its tail closed.

CHAPTER 12

TAIL FANNING AND FLICKING

12.1 INTRODUCTION

The use of "Tail fanning" and "Tail flicking" by many species of *Rhipidura* has been noted by a number of researchers (Buller 1882, Delacour and Mayr 1946, Masefield 1948, Bailey 1955, Westerskov 1967). However, none has provided detailed descriptions of these postures and very few suggestions as to their function have been made. Some ornithologists have vaguely associated these tail actions with a display (Anderson 1926, Smythies 1960, Diamond 1972), and others believe that for some species it is a means of "Flushing insects" (Warham 1956, Brockie 1971, Harrison 1975).

A detailed study on the nature and function of "Tail fanning" and two types of flicking form the basis for this chapter. "Tail fanning", "Vertical flicking" and "Tail flashing" are described and discussed separately.

12.2 TAIL FANNING

The Grey Fantail has a tail length of approximately 75 mm (Rand and Gilliard 1965). The tail consists of 12 rectrices which are fully fanned under some circumstances (Plate 5) but closed to a width of two rectrices under others (Plate 6). This section is based on 596 observations of "Tail fanning".

12.2.1 Methods

Standard observations on "tail fanning" were taken throughout the 12 month period and included:-

(i) the activity of the bird,

(ii) the presence or absence of tail fanning,

(iii) the position (i.e., height above the ground) of the bird in the branches,

(iv) the type of ground cover the bird moved over, and

(v) the change in behaviour that occurred as the tail fanned open.

From these observations it was possible to relate fanning to specific activities and an indication of the stimuli evoking fanning could be made.

12.2.2 Results

The fantail usually spread its tail as it "Waltzed" along the branches. The tail, which was held between 0° to 45° above the level of the back, remained fanned during these movements. Fanning also occurred when the bird hung upside down on the underside of branches and when moving vertically up tree trunks. It occurred less frequently when the bird gave "Type 1" calls while standing below silvereyes and before "Hawking forays" (Table 46).

Fanning did not appear to accompany such maintenance activities as preening, perching, bathing, "Bill-wiping", or manipulating and eating prey, nor was it associated with "Type 2" or "Type 3" vocalisations.

When the fantails approached and stood near me, "Tail fanning" was not evident until they started moving along the branches. The action was absent from most of the courtship displays, i.e., "Courtship feeding", "Wing-shivering" or copulation, and was not pronounced when the birds stood or fed close to each other (Table 46).

TABLE 46. Activities associated with "Tail fanning"

Activity	Total number of observations of each activity	Number of fanning observations	Percentage frequency of fanning observations
Preening	40	3	7.5
Manipulating or eating prey	19	4	21
Perching	125	12	10
Bill-wiping	11	1	9
Making "Type 1" call	30	13	43
Making "Type 2" vocalisations	21	0	0
Making "Type 3" vocalisations	49	12	24
Interacting with me	34	3	9
Interacting with conspecifics	13	2	18
Interacting with silvereyes	46	25	54
Upside down posturing	65	65	100
Standing before hawking forays	31	16	52
Pivoting	27	6	22
Courtship feeding	115	0	0
Copulating	13	1	8
Wing shivering	15	1	7
Foraging in the branches	447	425	95
Foraging on the ground	228	77	34
Total	1329	596	

There was a significant difference in fanning while foraging over the branches and on the ground ($\chi^2 = 513$, df = 1, $p > 0.001$). The amount of fanning on the ground was correlated with the type of ground cover (Table 57). That is, on the flat ground surfaces such as paths, grass, and areas of leaf litter, fanning did not usually occur but when the fantail moved among exposed roots, vines, twigs, fallen trees and logs there was a significantly greater amount of tail fanning ($\chi^2 = 72$, df = 1, $p > 0.001$).

TABLE 47. "Tail fanning" on the ground.

Type of cover	Total number of observations	Number of observations in which fanning occurred	Percentage frequency of fanning observations
Flat ground, i.e. grass, paths, leaf litter	177	39	22
Branches, twigs, flax leaves, roots, vines	33	25	76
Fallen trees or logs	18	13	72
Total	228	77	

"Tail fanning" while foraging did not appear to be restricted to any specific level of the bush (Table 48).

TABLE 48. The relationship between "Tail fanning" and the foraging level.

Foraging level	Number of feeding observations	Percentage frequency of fanning
Lowerstorey	148	97
Middlestorey	157	94
Upperstorey	118	93
Canopy	24	92
Total	447	

The following activities were noted frequently, and give some insight into the function and stimuli evoking fanning.

(i) The tail was not fanned as the bird sat giving "Type 2" vocalisations, but as soon as the fantail started moving along the branch the tail fanned.

(ii) The tail was not fanned on landing, but opened as soon as the bird moved along the branch.

PLATE 7. The downstroke of the fanned tail during take-off.

(iii) While preening, the tail was closed until the bird turned on a branch.

(iv) Whenever the bird turned on a branch the tail was spread.

(v) If the bird jumped on to a swinging vine the tail fanned.

(vi) When a fantail hopped from one perch to another the tail was fanned.

A study of several cinemagraphic films showed that fanning also occurred:-

a) during "Vertical tail flicks (Section 12.3). The tail was fanned when it was raised to a position perpendicular to the body.

b) before take-off.

c) during the downstroke of the tail, as the bird took-off (Plate 7).

12.2.3 Discussion

The results of this study suggest a relationship between fanning and foraging activities. "Tail fanning" is not a component of courtship displays as it frequently occurred when birds were alone.

Although fanning is associated with foraging, what is its exact function? There appear to be two possibilities.

(i) The movement of the fanned tail from side-to-side may scare insects into flight, i.e., insect flushing.

(ii) It may be related to the mechanics of movement.

The first hypothesis was suggested by Harrison (1975). It was based on the fact that when Grey Fantails were feeding in fairly open, leafless shrubs the tail was held lower and only partly spread, "but as soon as the birds were among leafy foliage the tail was fully spread in a broad fan, erected vertically above the back and moved jerkily". He suggests that the vigorous movement of a large and conspicuous object among twigs and foliage" scares insects into flight. However, he does not provide any other evidence which would help substantiate his theory.

No mention is made of:-

(i) the effect of fanning, i.e., did fanning usually result in increased prey capture?

(ii) the effect of foliage disturbance, i.e., was it highly correlated with prey capture?

(iii) the amount of fanning on the ground, or

(iv) other activities associated with fanning.

In this study I have attempted to answer the questions that arose from Harrison's study. In doing so I have come to the conclusion that fanning does not function in "Flushing" insects. Some of the points on which I have based this conclusion include:-

(i) the fact that "Tail fanning" occurred continuously (i.e., the tail remained open) as the bird moved along the branch. I suspect that a rapid closing and opening of the rectrices would be more effective in flushing insects, but this was not observed,

(ii) very few hawking forays after apparently flushed insects were noted,

(iii) if "flushing" was the function, why did "Tail fanning" occur when the bird was moving over the flat, but not uneven ground? and

(iv) foliage disturbance by the movement of the fanned tail was not seen in this study. In fact, the bird often closed its tail as it moved through dense foliage and vines.

I believe that fanning has three basic functions which are related to movement. Firstly, in flight, fanning is used to steer the bird in any direction to act as a brake, to form a slot behind each wing and increase lift till the bird gains speed and as a means of increasing the lifting surfaces (Storer 1948, Thomson 1964, Welty 1964, Van Tyne and Berger 1966). These effects are accentuated in long-tailed birds and provide a great asset in aerial manoeuvres (Thomson 1964).

Therefore, fanning during the flight of the fantail probably acts as a rudder enabling the bird to change direction suddenly in pursuit of its prey. This could be the main function in the summer months when "Aerial feeding", which involves a large amount of acrobatic manoeuvres, is the most common method of prey capture (Section 9.3.3).

Secondly, it aids movement from branch-to-branch (by hopping). Andrew (1956a) noted that during a jump the tail of passerines is usually spread and lowered, thus helping in directing flight. This appears to be the case with the fantail also. I feel that, more importantly than directing the flight, the downward movement of the fanned tail aids take-off by providing a greater thrust than an unfanned tail would.

Thirdly, it functions as a balancing device. The fantail moved along the branches by alternately placing one foot directly in front of the other. This resulted in a twisting of the body from side-to-side (i.e., "Waltzing", Section 9.3.2a). Instability of a bird in flight is usually corrected by fanning and tilting the tail (Sherwood 1946). I suspect that instability arising from the turning movements involved in "Waltzing" is also counter balanced by "Tail fanning". Because turning occurred continuously (i.e., as the bird finished swinging to one side, it swung back to the other), the tail remained fanned. An analysis of cinematographic films on "Tail flashing" (Section 12.4.2) showed "Tail fanning" to be related to turning and provides additional proof to support the theory of its role as a balancing device.

The relationship between fanning and specific activities can be explained by considering the last two functions. Those activities highly correlated with fanning, for example, "Type 1" calls (Table 47) and foraging in the branches, were ones in which movement was involved. The lower incidence of fanning is probably due to the fact that the bird

Four hundred and eighty-nine observations of "Vertical tail flicking" were noted.

12.3.1 Methods

A study of "Vertical tail flicking" was made throughout the 12 month period. The following points were recorded:-

(i) the behaviour of the bird before and after "Vertical flicking",

(ii) the relationship of "Vertical flicking" with prey capture. I recorded the success or failure of prey capture after flicking and the number of occasions prey capture occurred without flicking, and

(iii) the frequency of "Vertical flicking" as the bird moved through the branches and over the ground. A method employed by Andrew (1956a) while studying tail flicks in *Emberiza* was used. He observed birds for 10 to 15 minutes as they moved between branches and perches. Fantails seldom remained in one place for this length of time so I recorded the number of "Vertical tail flicks" during 15 second intervals. Data obtained in periods when the birds were definitely alarmed or when perched were discarded.

12.3.2 Results

"Vertical tail flicking" frequently occurred after, or while the bird was moving along the branches with the tail fanned and held between 0^{o} to 45^{o} above the level of the back. "Vertical flicking" was most obvious during the movement up branches, close and parallel to tree trunks. The bird would flick its tail and hop almost vertically to a branch directly above. "Vertical flicking" was also given frequently as the bird:-

(i) moved through the branches,

TABLE 49. The relationship between "Tail fanning" and foraging activities in some species of *Rhipidura*.

Species	"Tail fanning"	Comment	Reference
Dimorphic rufous Fantail *(Rhipidura brachyrhyncha)*	Present	Tail always raised and widely fanned. Bird continually moving through the middle spaces and undergrowth.	Rand and Gilliard (1965)
White-breasted Thicket Fantail *(B. leucothorax clamosa)*	Present	Not a forest bird but remains inside the densest and most tangled thickets. It adopts an exaggerated fantail posture with the tail fully spread.	Diamond (1972)
Black Fantail *(R. altra altra)*	Present	Usually solitary and has a typical Rhipiduran behaviour, displaying with fanned tail tail spinning about 180° on its perch.	Diamond (1972)
Chestnut-bellied Fantail *(R. hyperythra muelleri)*	Present	A middlestorey forest fantail. Habit of tipping forward, nervously fluttering its wings and fanning its tail, then spinning 180° to repeat the performance.	Diamond (1972)
Northern Fantail *(B. rufiventris)*	Absent	Seldom fan their tails, and flutter much less. They perch in a more upright positon and tend to fly after insects and return to the same exposed branch many times, whereas grey fantails flit restlessly from perch to perch.	Frith (1976)
Friendly Fantail *(R. albolimbata)*	Absent	Sits with tail raised above the wing tips, but rarely fans its tail. Less active, stays on a single perch and flys out to catch insects.	Rand and Gilliard (1965)

is more stable. The fantail tended to run quickly over flat ground, with the tail closed and held approximately 60 above the level of the back. As soon as the bird moved over uneven ground (i.e., twigs, fallen branches, exposed roots) the bird's tail fanned open and "Waltzing" began. If "Flushing" was the main function of "Tail fanning" it would surely occur regardless of the evenness of the ground.

The relationship between "Tail fanning" and feeding below silvereyes or before "Hawking forays" is interesting. Here "Flushing" was not required because food was supplied by the silvereyes or consisted of prey already in flight. Therefore, fanning does not seem to be related to flushing in these situations. Instead the tail is probably spread to provide maximum thrust for take-off as the bird flies out to catch its prey.

An analysis of the literature on other species of fantails suggests a relationship between fanning and movement through the branches. By comparing the type of foraging activities with the amount of fanning it is found that fanning is most pronounced in those species which continually move through the canopy (i.e., Dimorphic Rufous Fantail, White-breasted Thicket Fantail, Chestnut-bellied Fantail and Pied Fantail Flycatcher), and virtually absent in those birds (Northern Fantail, Friendly Fantail and White-throated Fantail) that are less active and stay on a perch, from which they fly out to catch passing insects (Table 49).

12.3 "VERTICAL TAIL FLICKING"

"Vertical tail flicking" is the term I use for the movement of the tail from a position slightly below or above the level of the back to one perpendicular to the body. It specifically refers to movements which take place within 1/18 second.

(ii) fed below silvereyes, and

(iii) hung upside down on the branches.

"Vertical tail flicking" appeared to occur more frequently on the branches than on the ground. Very few observations of this action while on ground were made. In a study of 52 fifteen second intervals of ground feeding there was no "Tail flicking" on 73% of the occasions and only one or two flicks were observed during the other 27%. In 28% of 43 observations there was no "Vertical flicking" on the branches and as many as nine flicks were recorded (Table 50).

TABLE 50. Number of "Vertical tail flicks" per 15 second interval on the branches and on the ground.

Number of flicks per 15 second interval	Number of observations		Percentage frequency of observations	
	In the branches	On the ground	In the branches	On the ground
0	12	38	28	73
1	5	10	12	10
2	7	4	16	8
3	7	0	16	0
4	5	0	12	0
5	1	0	2	0
6	3	0	7	0
7	0	0	0	0
8	1	0	2	0
9	2	0	5	0
Total	43	52	100	100

Flicking often occurred on bare branches and the movement rarely disturbed the surrounding foliage. "Vertical tail flicking" was rarely observed during courtship displays, preening, bathing, perching, interactions between fantails, or pivoting activities.

After the tail flick the bird hopped to a branch 30 to 90 centimetres away in 85% of 489 observations, but occasionally (13%)

stood still for several seconds. The bird rarely pecked at a branch or caught prey after the flick (Table 51).

TABLE 51. Behaviour after "Vertical tail flicking"

Behaviour after "Vertical tail flicking"	Number of flicking observations	Percentage frequency of flicking observations
Remained standing	62	13
Hopped to another branch	415	84
Caught something	4	1
Pecked at a branch	4	1
"Bill-wiped"	4	1
Total	489	100

"Vertical flicking" was more frequently followed by movement to a higher perch (Table 52) than a lower one, i.e., the fantail moved significantly less frequently downwards after "Vertical flicking" than upwards and to the side ($\chi^2 = 240$, df = 1, $p > 0.001$).

TABLE 52. Direction of movement after "Vertical tail flicks".

Direction of movement after "Vertical Flicking"	Total number of "Vertical flicking" observations	Percentage frequency of flicking observations
Movement upwards	201	48
Movement to the side	118	28
Movement downwards	96	24
Total	415	100

Although flicking was usually followed by movement to other branches the bird frequently hopped without flicking. However, the tendency to flick before hopping was greatest when moving up, slightly less when moving to the side, and quite low when movement was directed downwards (Table 53).

TABLE 53. The presence of "Vertical flicking" before movement.

Direction of movement	Total Number of observations	Number of observations in which flicking preceded movement	Percentage frequency of flicking observations before movement
Upward	43	34	79
To the side	46	25	54
Downwards	29	10	34
Total	118	69	

An investigation of "Vertical flicking" and prey capture revealed the following points:-

(i) flicking was rarely followed by prey capture, i.e, flicking without catching prey occurred significantly more often without catching prey than flicking followed by prey capture ($\chi^2 = 68$, df = 1, $p > 0.001$), and

(ii) the bird frequently caught prey without flicking (Table 54).

TABLE 54. The relationship between "Vertical flicking" and prey capture.

Relationship between "Vertical flicking" and prey capture	Number of observations	Percentage frequency of observations
"Vertical flicking" followed by prey capture	8	6
"Vertical flicking" without catching (or attempting to catch) prey	54	40
Capture of prey without flicking beforehand	72	54
Total	134	100

12.3.3 Discussion

"The conspicuous spreading and movements of the tail of typical

Rhipidura species, including the Grey and Rufous Fantails, are similar to the plumage display that in other birds are associated with agonistic displays" (Harrison 1975). In my study, "Vertical tail flicking" was not involved in interactions between South Island Fantails and was frequently given by solitary birds. Therefore, flicking does not appear to function as a display. Some ornithologists believe that "Vertical tail flicking" is a means of "Flushing" insects (Brockie 1971, Harrison 1975). A number of arguments against this theory have become apparent during the course of this study and include:-

(i) the fact that the bird frequently caught prey without flicking,

(ii) that the bird often flicked without catching prey, and

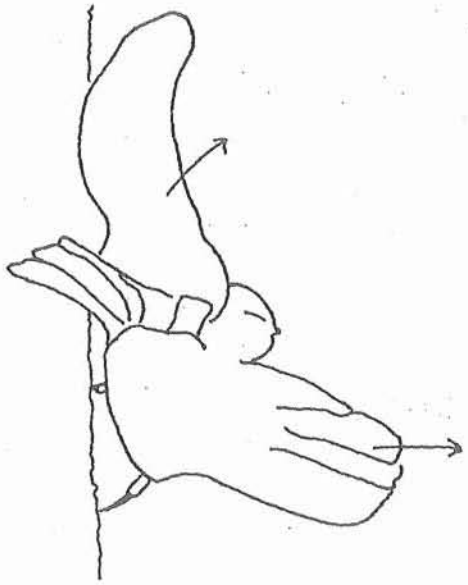
(iii) that the bird flicked in circumstances not related to prey capture. These circumstances included:-

a) the movement of a bird, with its bill full of food, towards the nest. As the bird approached, it often landed on branches before entering the nest. The bird would vertically flick its tail before flying to a nearer perch. In these circumstances, when the bird's motivation to feed the young is presumably high, why or how could the motivation to "scare" and capture prey also be high?

b) feeding below silvereyes. Here the fantails were feeding on prey stirred up by the silvereyes' movements. Flicking occurred frequently before hawking forays out to catch food that dropped below the silvereyes, not from the fantail's activity. If "Vertical flicking" functions to "Flush" insects why perform it unnecessarily, i.e., when food is supplied by another means?

The "Flushing" theory may have held some weight if the flicking disturbed the foliage around the fantail, but in this study it rarely

4 – 11



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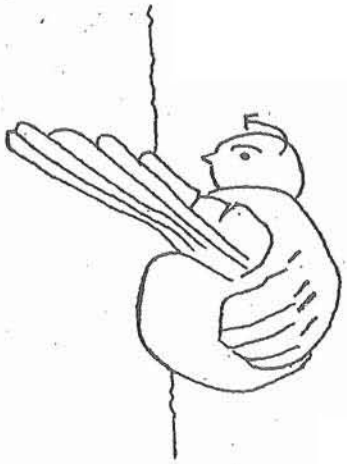

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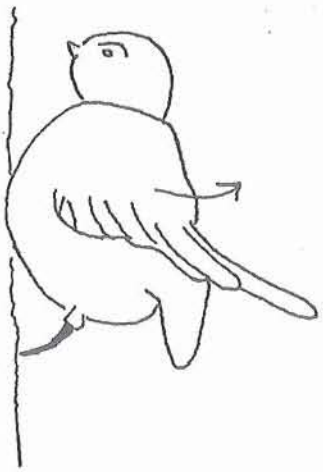

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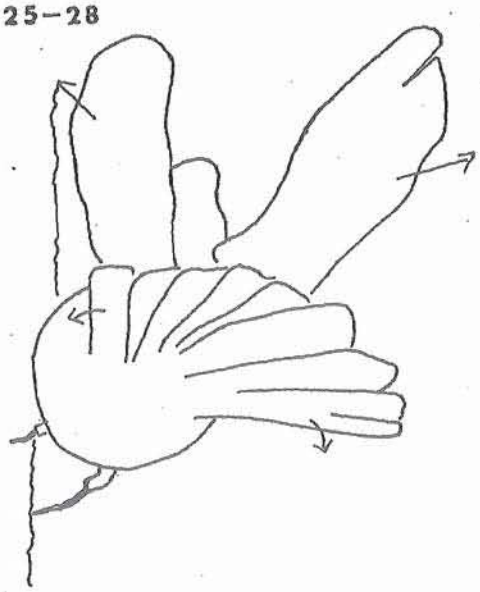

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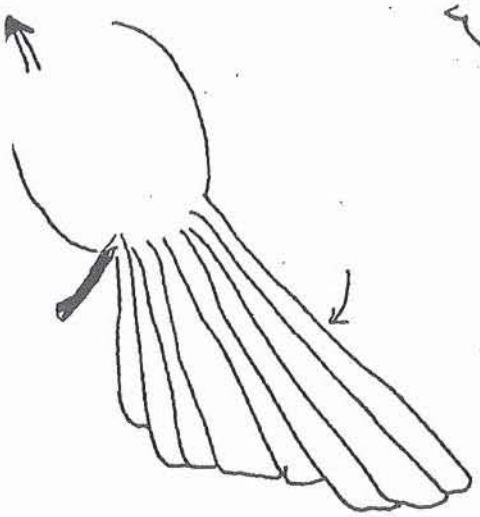

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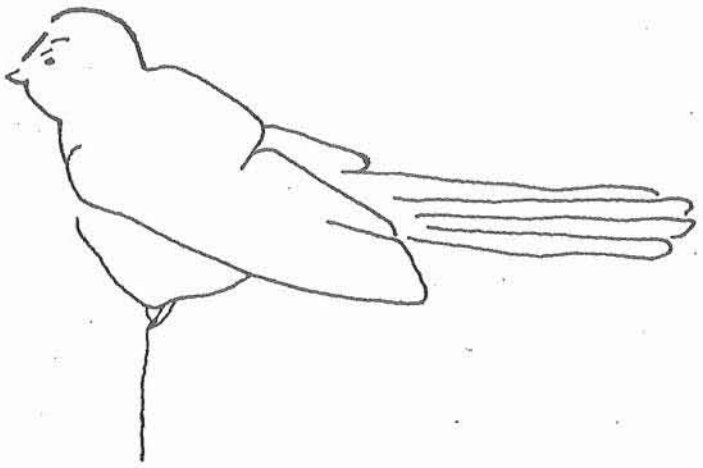

(Filmed at 25 fps.)

FIGURE 25. Fanning and lowering the tail during movement up a tree-trunk. In Frames 4-11 the wings are flicked as the bird turns its head (Frames 12-18). The tail is fanned out and wings flicked as the bird turns before hopping up the tree trunk (Frames 29-38). Note the fanned tail and lowering of the tail as the bird hops up the tree-trunk..

occurred and, in fact, flicking was often given on bare branches, twigs and tree trunks. Another method of disturbing the foliage and insects in it was used by the fantail. A bird often flew or fell through a clump of leaves, catching prey at the end of the fall (Section 9.3.2a). This appeared to be a very efficient and successful means of disturbing or "Flushing" insects and one wonders why a bird would employ an apparently unsuccesful, energy-wasting method, when it had evolved a more successful one.

Another query arises if one accepts a relationship between "Vertical flicking" and flushing insects. Why should there be a difference in the frequency of tail flicks on the branches and on the ground? If "Flushing" is the funct-on one would expect at least as much, probably more, flicking on the ground as on the branches. I suspect insect "flushing" is employed more by ground than arboreal feeders.

For these reasons I reject the "Flushing" hypothesis and suggest another function of "Vertical flicking". "Vertical flicking" positions the tail at an angle that will provide maximum thrust when it is lowered during take-off, whether it be to a nearby branch or to another tree.

Hinde (1955) associated "Vertical flicking" with a flying tendency, and Daanje (1957) noted that "many birds erect the tail just before jumping". "Vertical flicking" just before jumping was also apparent in this study. At the start of the take-off the tail was gradually lowered until it was almost in line with the body axis. At the same time the tail was spread to a certain extent (Fig. 25). Daanje (1957) suggested another function of "Vertical flicking". If the tail was kept in line with the body axis, the full weight of the tail would have to be carried right at the start. By first erecting and stretching the tail, its drag is coming into play gradually.

If "Vertical flicking" is related to movement from branch-to-branch, and functions to increase thrust, one would expect a higher

frequency of flicking during hops upwards or to the side (situations in which a large amount of thrust is required to lift the bird) rather than downwards where the weight force compensates the need for increasing thrust. The results illustrate this point (Table 52). My hypothesis, that is, that "Vertical tail flicking" is related to the movements of the fantail, explains some of the questions raised by the "Flushing" hypothesis. That is:-

(i) flicking occurred after the bird landed on a branch near the nest so that a maximum thrust was supplied for its final flight to the nest, and

(ii) flicking occurred more frequently on the branches than on the ground, because the bird continually hopped from branch to branch. Andrew (1956) found that species which fed by pursuing insects amongst branches had a significantly higher mean frequency of tail flicks than ground feeders. He suggested that the difference was probably due to the fact that they tended to travel more by flight.

For these reasons I believe that "Vertical tail flicking" aids locomotion from branch-to-branch by positioning the tail in such a way that it will provide maximum thrust and minimise the drag from the tail during take-off.

12.4 "TAIL FLASHING"

While "Tail flashing", the rectrices were repeatedly flicked out and closed, exposing the white outer feathers. The opening and closing of the rectrices occurred as frequently as three times per second, thus producing the characteristic "Flashing" effect. Sixty hundred and eighty-one observations of "Tail flashing" were recorded.

12.4.1 Methods

Two basic methods of studying "Tail flashing" were used:-

(i) analysis of cinematographic films. I took several Super 8 films (each frame being 1/40 s in duration with 1/18 s between frames), but most information was obtained from a 16 mm National Film Unit Production called the "Legend of the Birds" taken at 25 frames per second. Sketches were obtained from a frame-by-frame study of the film, and

(ii) field observations on the activities associated with "Flashing".

12.4.2 Results

"Tail flashing" was observed under a large variety of circumstances:-

(i) as the bird sang, usually while perched and pivoting from side-to-side,

(ii) while standing on the ground or on perches near the observer,

(iii) as the bird sat perched but looking around,

(iv) as the fantail collected nest material from the ground,

(v) when the fantail was perched near a thrush, between attacks on the thrush. The fantail usually stood pivoting giving fast, loud "Type 1" calls or "Type 2" vocalisations,

(vi) while perched and before "Hawking forays" or "Aerial feeding" flight, and

(vii) while standing on the nest-rim pivoting and giving the "Feeding vocalisation".

I never observed prey capture after "Tail flashing" so I doubt whether it is associated with insect "Flushing". It occurred throughout the canopy, on thin branches, horizontal tree trunks, fence wires, and on the ground. "Flashing" occurred in the absence of other fantails and myself (i.e., when I was out of sight).

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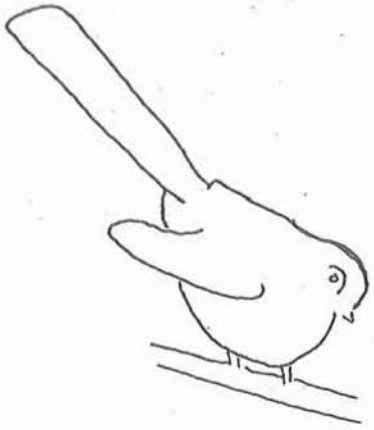
39 – 40

41 – 56



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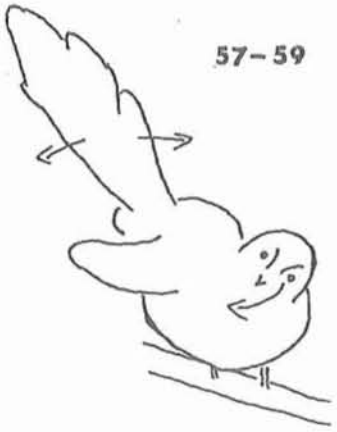

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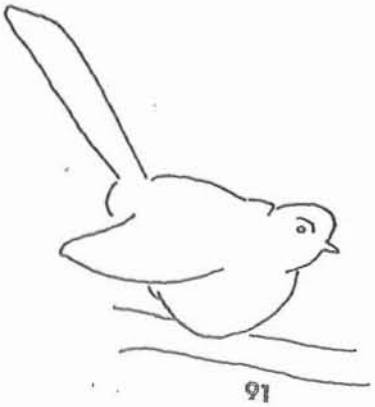

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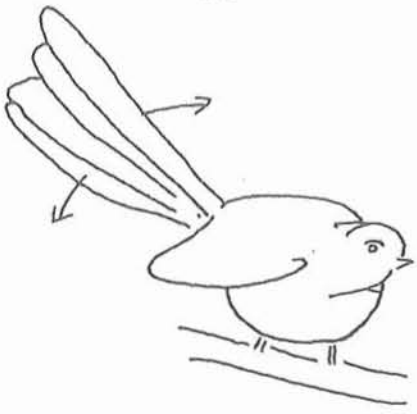

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(Filmed at 25 f.p.s.)

FRAMES

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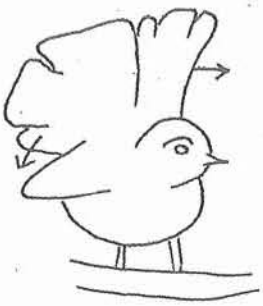

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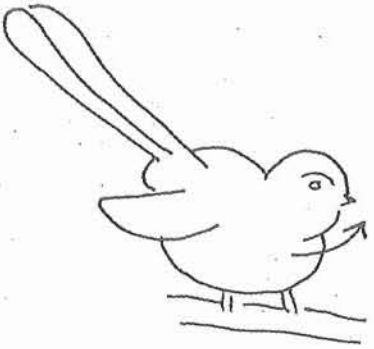

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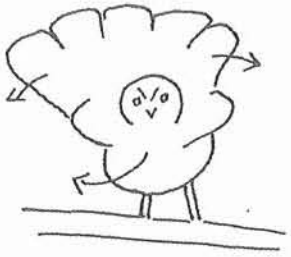

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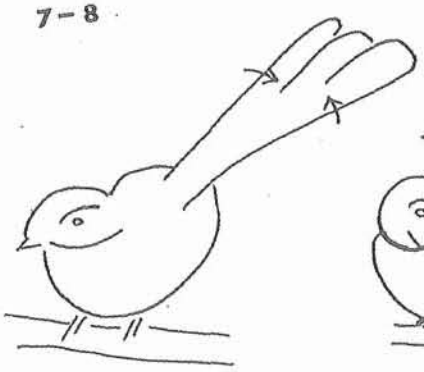

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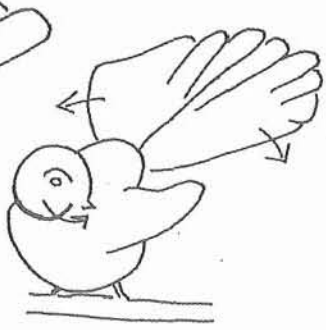

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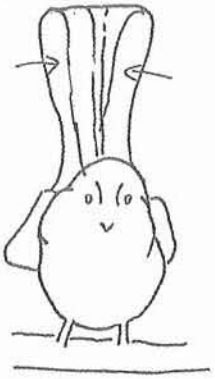

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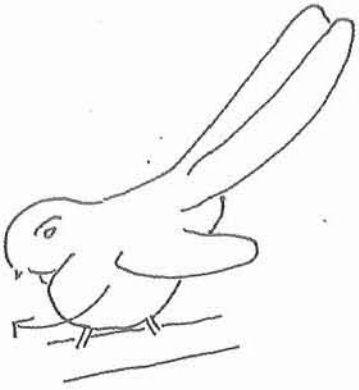

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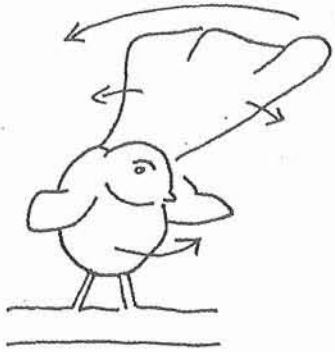

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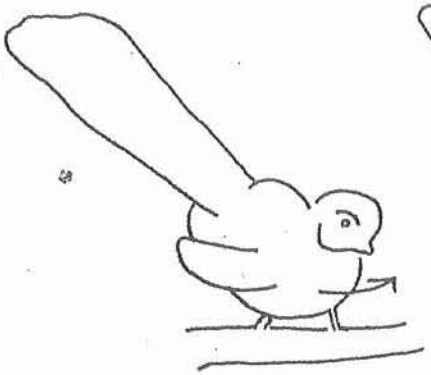

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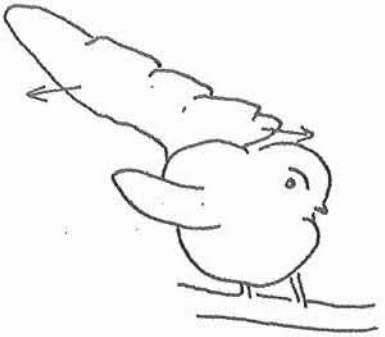

FIGURE 26. "Tail flashing". In most frames the tail fans out just before or as the fantail turns its head or body. See Frames 3, 9, 31 and 57.

"Flashing" was usually associated with a pivoting of the body from side-to-side which occurred:-

(i) before hawking forays and aerial feeding flights,

(ii) while feeding nestlings,

(iii) before "settling" during incubation and brooding spells, and

(iv) while standing on the ground.

An analysis of cinefilms on pivoting showed that an outward flick of the rectrices preceded a turn of the head or the body (Table 55). The bird occasionally flicked the rectrices out without moving (Fig. 26, Frames 10 to 15) and occasionally turned without flicking (Fig. 26, Frames 85 to 91).

TABLE 55. The relationship between an outward flick of the rectrices, in "Tail flashing", and movement.

The relationship between an outward flick and movement	Number of observations	Percentage frequency of observations
An outward flick, followed by a head or body movement	72	82
An outward flick, without movement	9	10
Movement without an outward flick	7	8
Total	88	100

In half the frames analysed the bird flicked the rectrices out as the head and/or body was turned, but in the other half flicking occurred a frame (i.e., 1/24 sec) before the bird turned (Table 56).

After turning, the tail was closed and there was a slight fanning between the frames. However, this never reached the extent of the full fannning observed before turns.

The bird turned as many as six times per second but usually turned at a rate of three times per second (Table 57).

TABLE 56. The relationship between the outward flick of "Tail flashing" and head and body movements.

Movements following outward flicks	Number of observations	Percentage frequency of observations
Outward flick with simultaneous head turning	24	33
Outward flick with simultaneous head and body turning	12	17
Outward flick with head and body turned afterwards	29	40
Total	72	100

TABLE 57. The number of turns per second as the bird pivots.

Number of turns/s	Number of observations	Percentage frequency of observations
1	2	5
2	4	11
3	12	33
4	6	17
5	6	17
6	6	17
Total	36	100

12.4 DISCUSSION

From my field observations it became apparent that "Tail flashing" was not a display, as it was given in the absence of other fantails and myself. I do not beleive that it is a means of "Flushing" insects for a number of reasons. Firstly, "Tail flashing" did not appear to be associated with prey capture. "Tail flashing" was often

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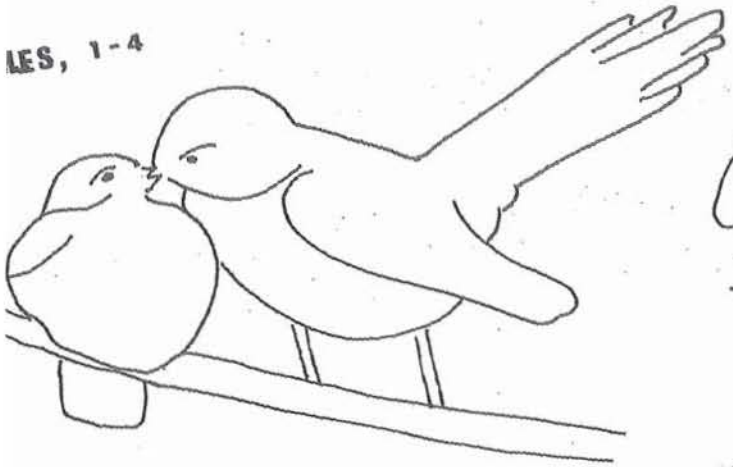

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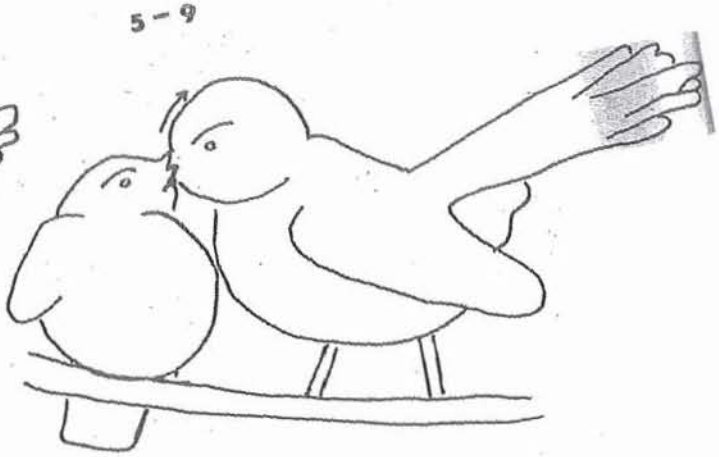

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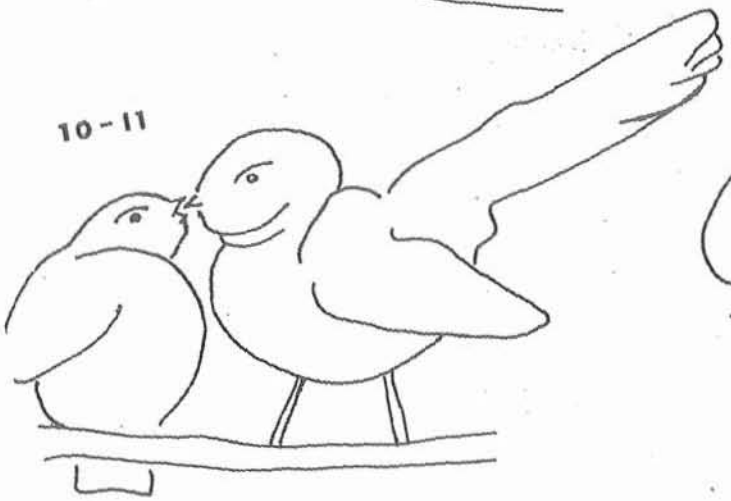

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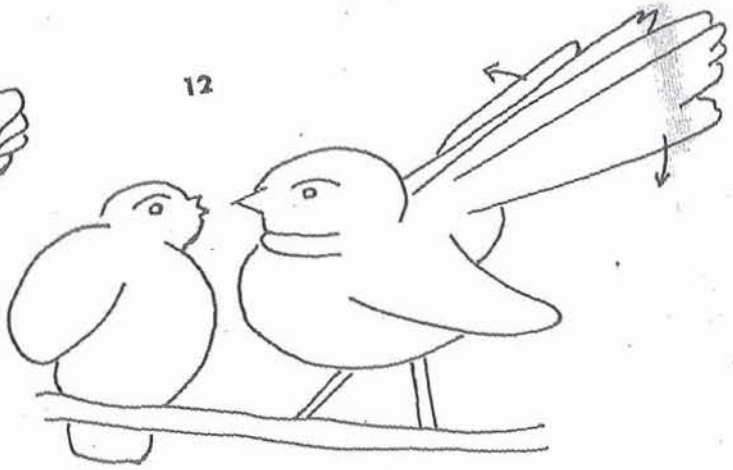

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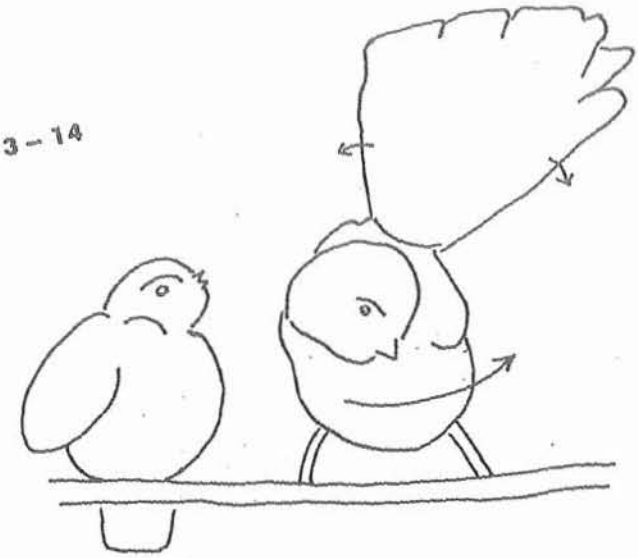

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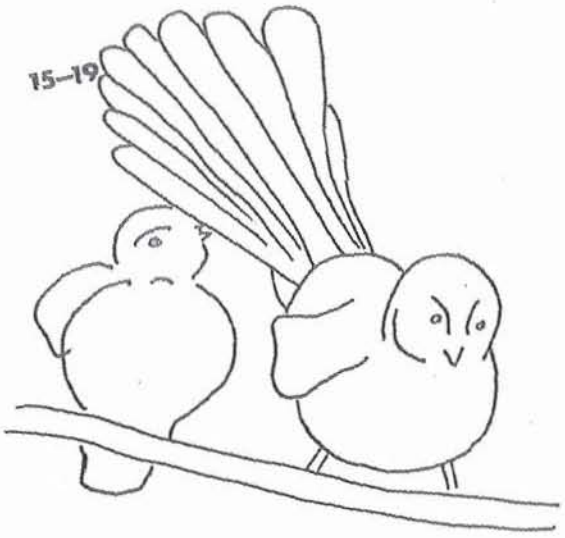

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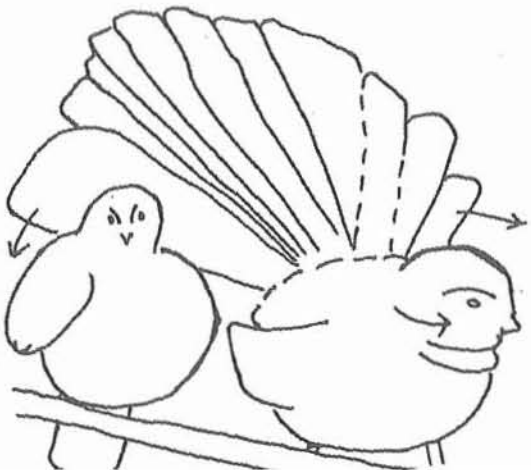

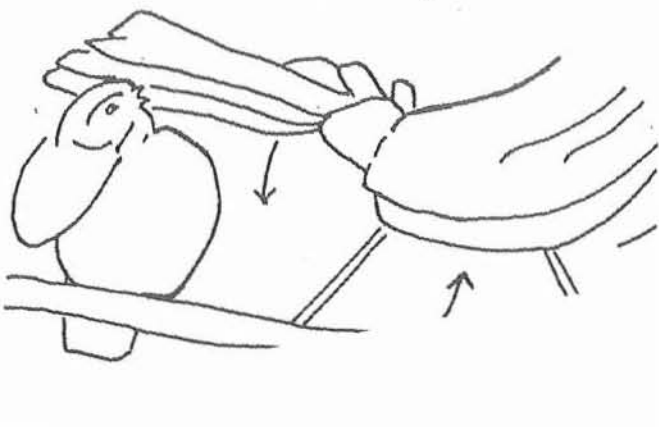

FIGURE 27. "Tail flashing" after feeding a fledgling. In Frame 12 the tail is fanned out before the parent turns (Frames 13 and 14). Although the tail is fanned slightly in Frames 15-19, it completely fans open as the fantail turns and prepares for take-off in Frame 21. Note the lowering of the fanned tail during take-off.

observed without the fantail catching prey and there were many instances when the fantail caught prey without "Flashing". Secondly, "Tail flashing" occurred in circumstances when the bird was obviously not feeding. For instance, why and how could "Tail flashing" function in flushing insects when it is performed on fence wires, in the nest, and as the parents fed fledglings (Fig. 27). In this sequence, "Tail flashing" occurred before the parent turned away from the fledgling (Frame 12) and as it turned its head (Frame 20). "Tail flashing" was frequently given as the bird pivoted before "Hawking forays" and "Aerial feeding" flights. Again, if "Flashing" functions to "Flush" insects into flight why do it when they are already in the air?

The analysis of cinefilms clearly shows that "Flashing" results from a turning of the head and body during pivoting activities. It probably functions as a balancing device counterbalancing any instability that may arise as the bird turns.

CHAPTER 13

CHAPTER 13

CONCLUDING COMMENTS

This study suggests that "Tail fanning", "Vertical flicking" and "Tail flashing" are not components of courtship or aggressive displays, a mobbing response and probably not part of a distraction display. Although I did not observe a distraction display in the South Island Fantail it is unlikely that one exists. I base this conclusion on the results of a study by Armstrong (1954) who found that injury-simulation (i.e., distraction displays) by breeding birds tended to be most accentuated when the nest was in open, unprotected sistuations, when the nest was on or close to relatively level ground and when nests were open and meagre. He concluded that there was generally a lack of injury feigning in tree nesters.

After a detailed study on feeding behaviour and tail fanning and flicking, I do not believe that "Tail fanning", "Vertical tail flicking" or "Tail flashing" functions in "Flushing" insects, a hypothesis put forward by a number of researchers. These activities are related to the mechanics of the movements used while foraging.

As had been the case with the function of the tail fanning and flicking in the *Rhipidura* genus, much controversy exists on the role of wing flicking in many passerine species. In particular, the function of wing-flicking in Mocking birds *Mimus polyglottos* forms the subject of recent debate. Some observers believe that the white wing patches exposed by flashing wings of foraging Mocking birds startled insect prey into revealing themselves (Hailman 1960). Several authors, however, have pointed out that some birds without wing patches also resort to

wing flashing and that securing prey might not be the explanation of the habit (Selander and Hunter 1960). Selander and Hunter (1960) suggested that wing flashing may be an agonistic or threat display. Horwick (1965, 1969) presents the most recent complete summary for this phenomenon. None of these researchers have considered wing-flicking to be merely a part of the general locomotory mechanism of birds. I believe that a study on wing-flicking in a number of New Zealand passerines, with this view in mind, may throw new light on the controversy. A number of "National Film Unit Production" cinefilms could provide valuable information on this topic.

I believe a number of other studies on the biology and behaviour of the South Island Fantail are warranted. These include:-

(i) a study on the breeding biology of the fantail. Information on the effect of various ecological and climatic factors on the breeding success and survival of the fantail,

(ii) a study on the migration (if in fact it exists) of the South Island Fantail. Many young and adult fantails have been banded at Kowhai Bush, Kaikoura, and a study on the migration of this bird is feasible. Population counts in Kowhai Bush and along the Kaikoura coast at various times of the year could provide information on seasonal movements of the fantail. A study of prey abundance at the localities chosen for population counts must be an integral part of this study, and

(iii) an investigation of the relationship between "Vertical tail flicking" and distance the fantail hops. If the fantail could be studied in captivity, a study on the frequency of "Vertical tail flicking" with respect to the distance and height a bird has to hop, could prove interesting. I believe that "Vertical tail flicking" occurs more frequently when hopping large, rather

than small distances.

In general many aspects of the behaviour and biology of the genus *Rhipidura* are yet to be studied. With the growing interest in the evolution of many Australasian passerines I hope a study of speciation in New Guinea, Australian and New Zealand Fantails will be undertaken in the very near future.

SUMMARY

SUMMARY

1) A study of approximately 30 fantails in the non-breeding season, and four pairs in the breeding season, was undertaken in Riccarton Bush and the Christchurch Botanical Gardens between March 1975 and March 1976.

2) A brief outline of the behaviour patterns throughout the 12 month period is given.

3) A number of displays were identified in the fantail and included: "Sexual pursuit", "Courtship feeding", "Body-contact", "Hop-over", Precopulatory, Copulatory, "Wing-shivering" and "Lateral head-swaying" displays.

4) The male fantail "Courtship-fed" the female during pair-formation and nest building on the ground at at all feeding levels, but "Aerial courtship-feeding" occurred infrequently.

5) The "Body-contact" and "Hop-over" displays were performed by both sexes during nest-site selection and nest-building stages.

6) Most copulations attempted were preceded by a precopulatory display by the female.

7) Although the "Lateral head-swaying" display was only given by the male and only directed towards the female, "Wing-shivering" was performed by both sexes during aggressive encounters between each other in the breeding season.

8) "Tail fanning", "Vertical tail flicking" and "Tail flashing" were

not components of the courtship and hostile displays identified.

9) The selection of nest-sites, which included native and introduced species of trees, were made by the female and male.

10) Both parents collected nest material from the ground near the nest and faced the outside of it with cobwebs.

11) At the start of the construction of the nest the parents alternated visits to the nest, one leaving as the other approached, but at the later stages of nest-building and when parents had dependent young from an earlier brood, the female played a greater role in building.

12) Nest-building movements included "Head-rim", "Body-presses", "Turning" and "Wiping" movements. On landing in the nest the bird performed "Head-rim" or "Wiping" activities rather than "Body-presses".

3) The re-use of a nest which was used to rear an earlier brood was noted.

4) Incubation periods of 13 to 14 days were recorded. There was no difference in the mean length of attentive spells between the male and female fantail, however, there was a general increase in the length of attentive periods from the start of incubation of the first clutch to the end of incubation of the second clutch.

5) Both parents made an average of three visits/h to their first nest and two visit/h to the second nest, however the number of parental visits to the nest per hour increased after hatching and there was a general increase in the feeding frequency of the young by the parents during the nestling period. In the later stages, as many as 45 visits were made to the nest each hour.

16) Before feeding nestlings, the parents pivoted and gave a "Feeding vocalisation" on the nest-rim.

17) For at least two days after hatching "nest attentiveness" was high but by the ninth day less time was spent brooding and more time feeding nestlings. The mean length of each brooding spell was seven minutes with a range of 0.5 minutes to 31 minutes. Both sexes shared brooding equally at the start of the nestling stage, but most is done by the female as the chicks got older.

18) The young were fed by both parents during most of the fledgling stage, but once the building of the second nest had begun the male did most of the feeding while the female sang.

19) A number of feather care and comfort movements were identified and described.

20) The fantails spent most of their time feeding in the branches although "Ground feeding" was observed frequently, particularly during the winter months. In the winter more time was spent in the lower levels of the bush, but in the summer months the fantails tended to forage in the higher feeding levels.

21) Five feeding methods were identified: "Active canopy feeding", "Hawking forays", "Aerial feeding", "Ground feeding" and "Tree-trunk feeding". "Aerial feeding" and "Hawking forays" were used more frequently in summer, than in winter, to catch prey.

22) Compared with "Hawking forays", "Aerial feeding flights" were of longer duration and incorporated a longer amount of aerial acrobatic manoeuvres. The mean time perched between successive flights was also longer.

23) When moving over branches and the ground, the fantail used prey disturbance techniques which did not involve "Tail fanning", "Vertical tail flicking" or "Tail flashing".

24) Large prey, which were swallowed whole, were subdued by knocking them against the branch or by pecking at the prey clamped against the branch by one foot.

25) In winter months the fantails were frequently observed feeding in association with other passerines, particularly small groups of silvereyes. The fantails perched below the silvereyes and caught insects stirred up by the silvereyes' movements.

26) Five calls, i.e., "Type 1", "Contact type 1", "Fast type 1", "Type 2" and the "Feeding vocalisation" were identified and discussed.

27) There is no change in the lengths of songs during the breeding season.

28) A large amount of dawn singing was noted in the summer months but as winter approached the frequency of songs given in the early morning decreased.

29) The female, who rarely sang, gave very short songs which were audible over very small distances. The female was observed "Duetting" with the male.

30) The fantail responded aggressively towards myself and other passerines during the breeding season, and occasionally in the non-breeding season.

31) A mobbing response, which did not include "Tail fanning, "Vertical

tail flicking" or "Tail flashing" was identified.

32) "Tail fanning" occurred as the bird "Waltzed" along branches, when hanging upside down on the underside of branches, when moving vertically up tree trunks, and before take-off.

33) There was a significant difference in the amount of fanning on the branches and on the ground. Although very little fanning was noted as the fantails moved over the ground, a significantly larger amount occurred on uneven surfaces compared with flat ground surfaces.

34) "Tail fanning" is not a means of flushing insects but aids movement from branch to branch by helping in directing the jump and providing a greater thrust than an unfanned tail would. "Tail fanning" also functions as a balancing device.

35) "Vertical tail flicking" was noted before the fantail hopped from one branch to another (usually to a higher perch) but was rarely observed during courtship displays, while feeding on the ground, and before prey capture.

36) "Vertical flicking" positions the tail at an angle that will provide maximum thrust when it is lowered during take-off, whether it be to a nearby branch or to another tree.

37) "Tail flashing" was given before "Hawking forays", "Aerial feeding flights" and while pivoting on the ground, branches and nest-rim. "Tail flashing" did not precede prey capture, was not a component of courtship or aggressive displays and was not a part of the mobbing response.

38) "Tail flashing" functions as a balancing device counterbalancing

any instability and may arise as the bird turns during pivoting activities.

ACKNOWLEDGEMENTS

REFERENCES

APPENDIX

ACKNOWLEDGEMENTS

I would like to thank Dr John Warham for critically reading the draft copy of this thesis and for suggesting ways of improving the presentation of my results. I greatly appreciate his supervision and operation of the sound spectrograph. I am indebted to Professor Knox for recommending an extension of the date at which this thesis was to be completed.

I am extremely grateful to: Ewan Fordyce and Brian Gill for reading parts of my numerous drafts and for some critical and constructive discussions; Nick Fox, for taking a live, tethered New Zealand Falcon into Riccarton Bush; and Mary Poulesland, for showing me five nests at Kowhai Bush, Kaikoura.

Special thanks go to Terry Williams for photographing the fantail in Riccarton Bush, and to Mr Sims, the photographer attached to the University Library, for developing the prints. I appreciate the care taken by Mrs A.J. Dellow over the typing of this manuscript.

Finally, I cannot find enough words to thank my mother, and particularly my husband, for their patience, understanding and encouragement. Without their encouragement this thesis may not have been completed.

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APPENDIX 1: Length of attentive spells by the male and female at Nest 3.

Length of the female's attentive periods (min)		
7.0	9.0	7.0
8.0	9.0	4.0
5.0	14.5	10.5
13.5	5.5	7.5
19.0	10.0	11.5
29.0	10.5	26.5
4.5	18.0	5.0
10.5	9.0	13.0
9.5	13.0	17.0
11.5	13.5	19.0
14.0	8.5	16.0

Length of the male's attentive periods (min)		
7.0	551.0	12.0
2.0	14.0	3.0
9.0	109.0	6.0
4.0	30.0	7.0
4.0	1.0	1.0
9.0	1.0	6.0
286.0	8.0	3.0
47.0	137.0	430.0
6.0	0.0	15.0
4.0	0.0	14.0
14.0	3.0	8.0
7.0	340.0	1.0
28.0	1.0	245.0
8.0	8.0	1.0
25.0	5.0	3.0
25.0	4.0	2.0
0.5	6.0	6.0

APPENDIX 2. Lengths of attentive periods of Nest 5 and Nest 6.

Lengths of attentive periods at Nest 5.		
7.0	6.0	13.0
5.0	3.0	12.0
8.0	2.5	5.0
13.5	2.0	15.0
19.0	9.0	6.0
29.0	9.0	12.0
4.5	14.5	6.0
10.5	5.5	6.0
9.5	10.0	17.0
11.5	16.5	9.0
14.0	18.0	5.0
19.0	9.0	10.0
17.0	13.0	13.0
5.0	13.5	7.0
9.0	8.5	4.0
9.0	16.0	10.5
26.5	11.5	7.5

Lengths of attentive periods at Nest 6		
20.0	20.5	5.0
17.0	19.0	13.0
10.5	13.5	5.0
23.5	17.5	8.0
26.5	19.0	10.0
11.0	27.5	6.5
7.0	12.5	7.0
8.5	20.0	0.0
17.0	15.0	0.0
20.0	17.0	0.5
20.0	13.0	
18.5	16.0	
14.5	58.0	
15.0	20.0	
22.5	26.0	
24.5	19.0	
12.0	22.0	

APPENDIX 3: Per cent attentiveness between 0900h and 1700h during the incubation period.

Nest	Date of Day 1	DAY															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
5	9/9/75	60	70	91	94	95	-	91.5	91	93	97.5	94	-	-	77	96	99
		180	240	115	223	180	-	152	104	119	121	120	-	-	219	124	116
6	15/10/75	63	70	91	96	94	99	-	69	99	99	91	92	-	96	-	100
		118	240	129	180	180	181	-	224	120	178	180	135	-	184	-	236
7	14/11/75	70	82	94	100	-	97	95	94	91	93	-	96	-	97	97	
		180	149	120	206	-	287	120	125	120	180	-	149	-	161	158	
13	21/10/75	56	80	93	94	96	91	-	-	100	-	99	-	99	98	100	
		146	120	102	120	180	126	-	-	118	-	145	-	177	120	180	
14	26/11/75	51	65	78	91	95	97										
		162	164	180	120	120	141										

APPENDIX 4. Length of time the female and male left Nest 6 unoccupied during nest relief.

Length of time the female left the nest unoccupied (sec)		
18	22	5
9	10	4
19	5	8
33	11	10
1	16	5
7	10	11
6	5	9
8	10	11
9	12	8
11	8	13
10	22	7
9	1	8
5	7	39
4	4	3
6	38	29

Length of time the male left the nest unoccupied		
31	378	3
6	3	5
52	22	2
337	9	3
17	40	22
5	20	8
37	42	8
13	184	77
19	23	5
23	166	143
10	630	7
10	0	20
20	4	19

APPENDIX 5. Change in the lengths of attentive periods during the breeding season.

Lengths of attentive periods (min) on 20/9/75	
2	11
19	13
13	14
8	15
12	

Lengths of attentive periods (min) on 24/10/75	
17	21
22	21
19	19
20	20
21	22

APPENDIX 6. Length of time the fantail is perched between consecutive hawking flights and consecutive aerial flights.

Length of time between "Hawking" flights (sec)		
4.8	8.2	5.2
13.2	1.5	0.9
1.2	1.0	1.6
1.2	1.5	1.4
8.6	1.8	4.2
6.1	1.3	0.8
4.5	2.3	
0.6	2.6	
1.2	2.1	
1.5	2.0	
2.4	20.4	

Length of time between "Aerial" flights (sec)	
17.0	3.3
12.7	12.1
36.8	11.4
9.3	13.6
39.6	13.9
39.3	17.0
13.7	12.6
13.2	28.4
9.6	
9.7	
2.0	

APPENDIX 7. Length of "Hawking" and "Aerial" flights

Length of "Hawking" flights (sec)		
0.7	1.6	0.9
0.8	0.6	1.1
0.7	0.6	1.9
0.9	1.3	1.4
1.2	0.5	1.3
1.3	1.1	1.4
0.8	1.6	0.9
1.2	1.6	2.4
2.0	0.8	0.5
1.2	1.0	0.6
0.8	0.0	1.2
0.7	1.8	0.5
0.9	1.3	0.7
1.6	2.5	0.8
0.8	1.0	1.0
0.5	1.2	1.1
0.8	1.0	1.5

Length of "Aerial" flights (sec)		
7.0	10.0	13.9
5.2	3.0	5.1
4.0	10.1	3.1
5.9	4.8	6.9
5.5	5.5	10.6
6.0	5.6	5.4
2.9	8.2	7.5
6.1	10.0	8.5
6.0	6.0	8.8
5.4	8.8	8.7
8.1	6.4	5.8
5.6	6.9	4.1
9.8	7.2	3.5
5.1	8.4	5.4
15.0	9.0	

APPENDIX 8. Diurnal variation in the number of "Type 1", "Type 2" and "Type 3" vocalisations recorded on 13 and 14 May 1975.

Time	Number of vocalisations		
	"Type 1"	"Type 2"	"Type 3"
0700 - 0800	21	12	28
0800 - 0900	182	4	11
0900 - 1000	330	3	5
1000 - 1100	280	25	15
1100 - 1200	65	13	7
1200 - 1300	136	29	8
1300 - 1400	174	1	1
1400 - 1500	186	15	6
1500 - 1600	163	2	3
1600 - 1700	326	8	5
1700 - 1800	55	4	3
1800 - 1900	61	0	0

APPENDIX 9. Seasonal variation in the number of "Type 1", "Type 2" and "Type 3" vocalisations

Month	Dates of two days from which results were obtained	Number of vocalisations heard between 0700h and 1900h		
		"Type 1"	"Type 2"	"Type 3"
April	2 - 3	1501	98	120
	10 - 11	1705	101	180
	18 - 19	986	89	170
	28 - 29	1509	94	118
May	3 - 4	1909	121	116
	13 - 14	1979	116	92
	00 - 21	892	88	53
	27 - 28	708	14	2
June	2 - 3	601	21	20
	12 - 13	747	16	31
	19 - 20	335	22	69
	28 - 29	547	33	6
July	3 - 4	394	5	4
	10 - 11	461	1	2
	22 - 23	45	0	0
	29 - 31	395	3	28
August	2 - 3	421	80	120
	10 - 11	1200	194	164
	20 - 21	590	20	32
	29 - 30	89	0	99
September	6 - 7	96	40	100
	13 - 14	61	8	92
	20 - 21	76	3	183
	29 - 30	87	16	180